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THE COMPARATIVE MORPHOLOGY OF THE ZOOCECIDIA OF CELTIS OCCIDENTALIS.*

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The purpose of the present paper is three-fold:

1. To present a survey of the known insect and mite galls of Celtis occidentalis L.
2. To elucidate the histology of the normal gall bearing parts of the hackberry and that of the galls.
3. To study comparatively the structures treated, pointing out any significant conclusions and generalizations that may be attained in such a study.

During the course of personally collecting nearly five hundred types of zoocecidia, the author early discovered that the hackberry and its galls would afford a favorable combination with which to prosecute some anatomical work as outlined above. Four orders of cecidozoons are represented on this species of tree, causing seventeen known kinds of galls, of which sixteen are described in this paper. These orders do not include the hymenoptera whose galls are better known than those of the other orders. The histology of but one of the galls here presented, has been described previously. Since only one species of Celtis occurs in the regions (Ohio and Kansas) from which the material was obtained, no problems of correlation with various host plant species were encountered.

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Neither Celtis occidentalis L. nor any of the known insects forming galls on it, are reported from Europe. Houard ([11], Vol. I, p. 367) mentions two mite and two aphid galls occurring on Celtis australis L. and one aphid gall on C. cretica L.

Most of the gall material and the pieces of the normal leaf and petiole were collected in the latter part of the summer to insure maturity, and were satisfactorily embedded in paraffine and aniline safranin and gentian violet were used in staining the serial sections. The one year old stem material was taken in mid-winter. The studies of the witches-broom, the psyllid stem galls, the lepidopterous stem gall and the structure of the normal stem were made from sliding microtome sections of alcohol hardened material. These were treated with iodine and mounted in glycerine, a method used by Brown and shown by him (not yet published) to give greater satisfaction in the case of woody structures, than the longer methods of embedding and staining. All drawings, histological in character, were made with the aid of a camera lucida or projection lantern.

About one-third of the work was done while the writer was on the teaching staff of the Botanical Department of the Kansas State Agricultural College, and he desires to express his appreciation of the kindly interest in the work on the part of Prof. H. F. Roberts and the other members of that department.

The remaining two-thirds of the work was completed in the Botanical Department of the Ohio State University under the direction of Prof. J. H. Schaffner, to whom the writer is indebted for many helpful suggestions, particularly in regard to the theoretical aspect of the subject.

It gives the author especial pleasure to acknowledge the very valuable assistance rendered by Mr. Forest B. H. Brown, of the Ohio State University botanical staff. His excellent grasp of plant anatomy has made possible a source of information and inspiration, upon which the writer has drawn heavily.

To Prof. Herbert Osborn, of the Ohio State University is due the hearty thanks of the writer for the loan of entomological literature.

Much work has been done on gall anatomy in Europe, but little as yet in America. The great majority of all the anatomical papers heretofore published have been general in character, dealing with many kinds of galls on many kinds of plants.

The present paper is perhaps unique in that it deals comparatively with practically all of the galls on one kind of plant, and with the normal tissues of that plant. The presentation of the histology of the normal plant parts will be given first.

HISTOLOGY OF THE NORMAL PLANT PARTS.

The discussion of the histology of the normal plant parts will be followed by the descriptions of the galls arranged under the proper insect order and family name.

The elucidation of the normal histology was deemed important, for it is necessary to have clearly in mind the results of normal differentiation to adequately understand to what extent the galls have deviated in their specific structure, from the normal plant characters.

The Leaf. (Pl. XII, Fig. C). The upper epidermal cells are comparatively large and bear externally a thick cutinous layer. Large cystolith cells (cys.) break the continuity of the typical epidermal elements. The expanded internal part of the cystolith shows the presence of the calcium carbonate in it by staining very lightly if at all, while the stalk and the round external knob takes the aniline safranin with avidity.

The palisade zone consists of two layers of cells, the inner being much less prominent and in places merging with the elements of the spongy layer so as to break its continuity. The spongy layer is relatively compact.

The fibro-vascular bundles possess a more or less definite bundle sheath, composed of highly elongated cells with evenly thickened walls. These are especially well developed above and below the bundle (Pl. XII, Fig. C, a). The xylem elements are the characteristic tortuous tracheides of the spiral type. The phloem cells are as in leaves generally of the thin-walled, more or less elongate, sub-cylindric form. The end walls often slant at an appreciable angle.

The under epidermis consists of cells somewhat smaller than those of the upper protective layer. The outer walls are sufficiently thin to permit the protoplasts to bulge them outward. The stomatal cells are minute, the pair being intercalated between the larger epidermal elements at their bases.

The Petiole. The petiole as seen in transverse section, shows the typical asymmetric orientation of the fibro-vascular bundles, which, taken collectively, form a crescent-shaped area, lying nearer to the stem side of the petiole than the outer side. A segment from the middle of this region is shown in detail (Pl. XVI, Fig. D), extending from the epidermis on the side away from the stem axis, to a point on the inner side of one of the bundles.

The cortical cells and the epidermal cells show definitely thickened walls; a non-lignified type of thickening, however. These walls possess simple pits (not numerous). Scattered bast fibres are found in the inner cortical region, whose walls are not as thick, however, as those of the stem.

The phloem and xylem show no special characteristics. Tracheae and tracheids make up the body of the xylem, the tracheids being larger than many of those found in the stem and those found in the leaf.

The Stem. Figs A and B, Pl. XII, show the transverse and longitudinal, radial sections, respectively, of the one year old stem in winter condition. The cork layer is of the common type. The phelloderm is one cell layer thick. True collenchyma is but weakly developed, consisting when found in a favorable section, of but a single layer of cells of the outer cortex, with thicker walls than those beneath it. Since the cortex cells inward as far as the scleride and crystal "sac" layer, have definitely thickened walls, the differentiation between them and the collenchyma is ill defined. These cellulose-thickened walls show minute inter-cellular spaces between, but the simple pits which doubtless are present in them could not be definitely demonstrated as were those of the petiole cortex.

On its inner side the zone of cells just described (primary cortex) is sharply delimited by a layer two or three cells thick (typically) containing two kinds of elements; sub-isodiametrical sclerides or stone cells and cuboidal to slightly tangentionally flattened cells, each containing a monoclinic crystal of calcium oxalate. See Figures labeled with abbreviations. This scleride-containing cylinder of tissue is of especial interest because similar types of sclerenchymatous elements occur massed in various forms in most of the galls to be described hereafter. The region of the nodes, (particularly best developed in the cortex of the "angle") shows these two kinds of elements developed in sub-spherical masses.

The bast fibre cylinder is differentiated directly next to the layer just described. Within the bast fibre zone a layer of small celled parenchyma forms a transition tissue to the phloem which latter is typical and will not be discussed in detail, other than to state that the outer phloem parenchyma as well as that of the medullary rays in the phloem region, contain numerous sphaer-raphides (calcium oxalate).

The cambium consists of the typical, tangentionally flattened brick-shaped cells, massed three to six cells deep before exhibiting differentiation.

In the xylem region wood fibres and tracheids of small diameter predominate. The tracheæ of both primary and secondary xylem are of the ordinary types. It might be noted in passing that the innermost tracheal element of the secondary xylem co-ordinates perfectly with the adjoining vessel of the primary xylem in the development of the transversely elongated bordered pits, which relate the two. The medullary ray cells in the region of the wood, shows the typical sclerenchymatized condition, with the walls containing numerous simple pits extending to the middle lamella.

The tracheids, whose distribution in the stem is variable are of particular interest in connection with this study, because of the fact that it is only this kind of xylem element which is found in the appendicular hemipterous and dipterous galls. In the stem they are of extremely fine structure, particularly those formed near the end of the season's growth, possessing spiral and split-spiral thickenings of very minute size.

Inwardly the primary xylem is bordered by some cylindrical elements with slightly thickened walls forming a transition tissue to the storage or "differentiated" pith, which forms the periphery of the medullary cylinder. The cells of this storage tissue possess as usual large numbers of simple pits.

The large celled pith is of interest, since an exactly similar type of parenchymatous tissue is found in many of the galls.

Older stems were examined showing the products of secondary growth, but nothing new or of a type which possessed additional significance relative to the problem in hand, was found. All of the galls on the hackberry are developed from the meristem functional in primary growth, the insects in all cases being unable to gain access to meristematic elements after the first cork layer has formed.

Callus was not grown and examined, since from much previous work it is evident that this type of homogeneous tissue, approximately the same for all plants, has no significance in relation to the gall problem.

Wound wood, however, was investigated, but nothing different was found from similar kinds of tissue reported in other trees. In none of the galls studied was anything found approximating in the slightest degree the condition of things characterizing wound wood. Such may be the case, however, as is shown by Stewart (31) in the gall of Andricus punctatus Bass. on the oak.

DESCRIPTION OF ZOOCECIDIA.

Thomas (32) has defined a gall as "a variation in the form of plants caused by a parasite." This definition, though rather widely accepted, is too indefinite and does not delimit certain irregular conditions in plants brought about through predaceous insects and intracellular fungi, conditions which are never associated with the word cecidium or gall. In the author's work on zoocecidia (nematode, mite and insect galls) he has found it possible to adhere to the following definition for zoocecidium: An hypertrophy (abnormal enlargement of single cells) or hyperplasia (abnormal proliferation of cells) of plant cells causally related to certain parasitic animals. Both hypertrophy and hyperplasia may go on in the same gall. The only cases which this definition does not cover are those in which the normal tissue suffers differentiation inhibition without evident hyperplasia or hypertrophy. These cases are extremely rare. The xylem region of gall 1, described in the present paper is an instance of this kind, but as the cortex suffers marked hyperplasia this case is not a true example. Cases of this sort in which the number and size of the elements is not increased, only their qualities have changed, are included by Küster (15) under "Metaplasias."

Küster (15, 16) in his Pathologische Pflanzenanatomie has given phytopathology an excellent classification of cecidia in general. All of the galls described in the present paper fall under his "Heteroplastic Tissues," that sub-division of hyperplasias which shows "definite quantitative increase of an organ, in which by abnormal cell division, tissues are produced, the single elements of which do not resemble normal ones.

If the tissue of the heteroplastically changed organs and parts of organs be compared with corresponding normal tissues, differences will be found in more than one connection; the abnormal tissues vary from normal ones in regard to size of the single elements, as well as to the degree and kind of differentiation."

In the mind of the writer, the "degree and kind of differentiation" of tissues is the most significant with particular reference to the form assumed by the heteroplastic tissues as opposed to the forms of similar tissues in the normal parts.

Heteroplasmas, Küster divides into two sub-divisions, "Kataplasmas (differentiation not widely different from the normal) and "Prosoplasmas" (differentiation definitely and specifically different from the normal). The acarinous and lepidopterous galls (one each) to be described hereafter fall under the first, while the hemipterous and dipterous forms are all excellent examples of the second.

In the description of the galls, the taxonomic characters will be presented first, followed by the discussion of the histology.

In conformance with a previous paper (Wells [33]) the new galls described are not named, but given a list number. As pointed out in that paper it is essentially unscientific to name an insect with only the gall at hand. No entomologist would feel justified in creating a species on the characters of a puparium or coccoon, for such a structure embraces but a small part of the total number of characters to be considered. Only the paleo-entomologist should have the privilege of dealing in fragments. While it can be shown that the specificity of the galls is related to the specificity of the adult insects, this relation is not a causal one, but is merely a relation established through the fact that both gall and adult insect have a common specific origin in the larva. If the entomologist is to properly describe his unit (species) he should have all of the differentiation products coming out at the end of the insect's ontogeny. Too frequently, the entomologist has ignored the gall as a "deformation," when it is often as specific as the antennæ in its form and structure characters.

KEY TO GALLS OF CELTIS OCCIDENTALIS.

1. Twig galls; twigs massed and showing enlargement of bases, witches broom. *Eriophyes* sp. (1).
1. Twig galls; aborted lateral twigs, isolated not aggregated, Lepidopterous gall, (2).
1. Twig galls; simple low, ovoid swellings on sides of twigs, *Pachypsylla* sp., (4).
1. Bud gall; an abnormal enlargement of bud, *Pachypsylla gemma*, (5).
1. Galls on leaves and twigs, if on latter very different from foregoing. 2.
2. Gall of petiole, pear-shaped, large, involving entire petiole, *Pachypsylla venusta*, (7).
2. Leaf gall, blister-like, projecting but slightly from either side of leaf, *Pachypsylla vesiculum*, (3).
2. Leaf and twig galls, projecting prominently; definite appendicular structures. 3.
3. Leaf blade only; definite concavity on side of blade opposite gall, *Pachypsylla mamma*, (6).
3. Leaf blade, petiole and twig galls, on blade never showing concavity on side opposite the gall; itonid galls. 4.
4. Galls definitely conic; body of gall contracted distally. 5.
4. Galls definitely obconic; body of gall contracted proximally. 8.
4. Galls definitely globular, *Cecidomyia* sp., (14.)
4. Galls otherwise. 9.
5. Galls with ends attenuate, 6.
5. Galls with ends truncate (small nipple in center) 7.
6. Galls small, 2–3 mm. long, base not prominently expanded, *Cecidomyia* sp., (11).
6. Galls larger, 3–5 mm. long, base prominently expanded, *Cecidomyia unguicola*, (8).
7. Galls coarsely pubescent; distal half rather sharply constricted from basal, *Cecidomyia* sp., (13).
7. Galls smooth; distal half not constricted from basal half; stoutly conic, *Cecidomyia* sp., (12).
7. Galls smooth, larval chamber falls from the socket-like base. *Cecidomyia* sp. (16).
8. Gall sub-balloon-shape; basal half definitely constricted from distal expanded half, coarsely pubescent, *Phytophaga celtiphyllia*, (9).
8. Gall top-shaped; basal half not definitely constricted from distal half, finely pubescent, *Phytophaga wellsi*, (10).
9. Gall greatly flattened with central nipple; more or less prominent vertical, peripheral ridges present. (See end of introduction to the descriptions of the Itonididæ galls).
9. Galls relatively large, with very prominent, vertical, wing-like ridges projecting from the body of the gall, *Cecidomyia* sp., (15).
9. Galls generally in masses, larval chamber eventually loosening and dropping from the basal parts, *Cecidomyia* sp., (16).

Fam. ERIOPHYIDÆ. (Ord. Acarinæ).

This family includes the vast majority of the gall-forming mites. The galls are of simple types, though exhibiting great diversity. Most of the mite cecidozoons affecting the American flora, are undescribed, a condition related to the fact of their minute size and soft body, characters which demand a special technique to handle them. The majority of gall makers are members of the genus Eriophyes.

1. **Eriophyes** sp. This gall, a typical witches-broom, (Pl. XIX, Fig. 1) represents a more or less serious disturbance

of growth at the nodes. An excessive number (2 or 3 generally) of abnormal (wood reduced, pith increased) branches are produced from the same bud, followed by the development of an indefinite number of buds, all closely sessile in a mass at the node between the "gall" branches (Pl. XIII, Fig. 1). The subsequent infection of the basal buds of the new branches, the buds nearest to the original node attacked, accounts in great part for the characteristic irregular massing of the branches. If a young "broom" be stripped of its bark, (Pl. XIII, Fig. 1a), this relation of the primary and secondary branches is made evident. Often, however, in later years, buds located at the base of the primary "gall" branches will develop a shoot. After a number of years the mass of branches becomes so large as to be very conspicuous and unsightly. The author has investigated new branches growing on old galls without finding any mites. It seems probable that the condition of things grows worse after the primary infection, whether or not the mites are present.

The gall proper is altogether confined to the nodes affected, in which region two prominent facts stand out in relation to the histology of the parts affected: (1) The bases of the gall branches have suffered an inhibition of their differentiation; (2) The cortex shows definite hyperplasia. These facts are shown in Pl. XIII, Fig. 1c, which illustrates the longitudinal section of the part indicated at c, in Fig. 1a, which is a longitudinal, median section through a primary "gall" branch and the normal twig, from which it has grown out. The condition of the xylem is an extreme case of differentiation interference. Note the medullary ray cells are not very unlike those bordering it, cells which should have become wood fibres and tracheids, but which remain iso-diametrical, possessing simple pits scattered in the somewhat thickened walls. The co-ordination of the tracheæ, which do form, with the cells adjoining them by means of bordered pits, is not interfered with (Pl. XIII, Fig. 1 d).

Different branch bases show a wide variation in the degree with which normal differentiation has been checked. The extreme cases are almost uniformly composed of iso-diametric, simple-pitted cells, the thickening of the cell walls characterizing the pith region with as much intensity as the xylem. The least affected cases will show numerous vessels and tracheids, but few if any wood fibres. This variation is undoubtedly related to the degree of differentiation attained before the advent of the mites in the spring growth period.

The hyperplasia of the cortex of the branch base is a constant character. The stone cells are found aggregated into sub-spherical masses, a condition also true of the crystal bearing cells. These masses were much larger and more numerous than those found in the normal nodes, and often are found in juxtaposition (Pl. XIII, Fig. 1 c).

The cork developes a greater thickness than normally, but is not sharply defined from the primary cortical parenchyma. The elements of this latter tissue do not thicken their walls.

The above study is corroborative of Küster's (15) dictum that all witches-brooms, whether mite or fungus induced, exhibit an essentially undifferentiated condition.

Kellerman and Swingle (12, 13) have associated a fungus (Sphaerotheca phytoptophila Kell. and Sw.) with this gall. No mycelium was seen in the affected tissues; indeed none would be expected belonging to the fungus named, since its position among the Erysiphaceæ would indicate it to be wholly superficial, the haustoria only affecting epidermal cells. Other well known witches-brooms, particularly those of Europe, have been shown to be caused by mites only. One on Syringa is especially striking. See Abromeit (1). There can be no doubt that the kataplasma under discussion, is wholly induced through the agency of acarinous organisms.

Lepidoptera.

Practically all of the lepidopterous galls are of the stem kataplasma type. The larva works its way into the center of the stem and from that vantage point brings about important deviations from the normal sequence of events in the growth of the tissue. This is in marked contrast to the mite induced galls, for the mites occupy at first at least, an external position. Stem mite galls are known, however, which at length enclose the animals.

2. **Lepidopteron** (species undetermined). This gall, (Pl. XIX, Fig. 2) is an aborted shoot from a lateral bud, developing very rapidly in the early spring, reaching its full size (in Kansas) toward the end of April. 1½ – 3 cm. long, 4 – 6 mm. wide. The nodes near the end of the gall bear small leaves which die

early. Affected stems either smooth or pubescent. The larva finishes feeding on the central part of the galled twig and leaves the structure during the early part of May. It always eats out a circular hole near the base to make its exit. (Pl. XIII, Fig. 2 a). The gall soon after turns brown and drops from the parent branch.

Patton (26) has described a "hollow, elongate, twig swelling" from which he states cecidomyidous flies emerged "about the middle of June." From his brief description it is impossible to state whether his gall is the same as the one here described. The flies noted might have been parasitic on the lepidopteron.

Riley reports a tortricid, Proteoteras æsculana Riley, occurring on the hackberry. No mention of any gall is made, however, in connection with this tree, other than that the larvæ were found "on short twigs." On the buckeye and maple it "bores in the terminal green twigs, producing a swelling or pseudo-gall." (See Am. Nat. cit. below). This may be the insect concerned in the production of the lepidopterous gall herewith described, but from this mere suggestion of its gall forming habit, it is impossible to be certain.

Riley, Trans. St. Louis Acad. 4:321-322. 1882.
Riley, Am. Nat. 16:913-914. 1882.
Riley, 5th Report U. S. Ent. Comm. p. 609. 1890.

When studied histologically this gall is seen to be an excellent type of kataplasma (Pl. XIII, Fig. 2d). Sections of the normal and galled twigs are contrasted in 2b and 2c. The normal stem has suffered serious inhibition of its differentiation associated with marked hyperplasia. The xylem consists of but few primary and secondary vessels. The cambium is practically obliterated in the general mass of parenchyma formed. The bast elements never attain their ordinary heavy walls. The layer of stone cells with its accompanying crystal bearing elements does not appear at all. This study was made from material which had already begun to die back at the distal end, so that the condition found is not any stage of incomplete normal differentiation.

Fam. Psyllidæ. (Ord. Hemiptera).

The psyllidæ among hemipterous gall makers take third place, the aphididæ and coccidæ surpassing them in number of genera and species. Küster (17) reports seven genera from Europe. There are three known in America, the genera Livia, Trioza and Pachypsylla, which latter is confined in its gall forming habits altogether to the hackberry.

Five psyllid galls belonging to the genus Pachypsylla are herewith presented. The author concurs with Crawford (4, p. 111) in his monograph of the Psyllidæ, when he asserts that the following species of Pachypsylla erected by Riley (28) in the Fifth Rep't of the U. S. Ent. Comm., viz.: P. astericus, umbilicus, pubescens, globulus and curcurbita and P. rohweri Ckll, are "only variations of the species of P. mama, since the insects are said to be similar and the differences in the galls are not great." These species evidently represent intermediate forms between P. mama Riley and P. vesiculum Riley, though they are much closer to the former than the latter. The writer has noted the wide variation obtaining among the P. mama forms. The above named species will not be included in this paper, since their validity is rightly doubted. There are three species known other than those whose galls are dealt with in this paper, viz.: P. dubia, pallida and inteneris, but no galls are described with them. They are all said to be closely related to P. gemma Riley and may ultimately prove to be varieties of that species.

In the following studies diagrammatic presentation is resorted to in the elucidation of entire gall sections. Lignified tissue entering into the formation of the protective layers is shown by cross-hatching; simple stippling indicates parenchyma and the vascular bundles are outlined. The portions of the sections furnishing the diagrams used in detailed studies are outlined on the diagram.

3. **Pachypsylla vesiculum** Riley. This, the simplest of the psyllid galls, is a small (2–3 mm. dia.) monothalamous "blister" gall of the intervenal tissue, commonly found close to the principal veins of the leaf. They are apt to occur in great numbers. More or less evenly convex above; a small, rounded central papilla can be determined below. The galls, both above and below, become lighter in color than the normal leaf, though very green when young. Easily evident from the latter part of May on through the summer.

Riley, 5th Report U. S. Ent. Comm. p. 618. 1890.

The section of the gall in its position near a principal vein, is shown in Pl. XIII, Fig. 3. The convex zones of sclerenchymatized cells are very definite, extending over either side of the chamber, forming the protective envelope; protective in the sense that it has a real function in preserving the delicate nymph within from mechanical injury. At x, is observed the primary cone (now flattened) which grew up and around the young nymph and at y, the rounded papilla, which represents the original downward evagination, which lowered the larva to the center of the leaf, making possible the comparatively greater hyperplasia of the central mesophyll.

The histology of the left part of the section shown in the diagram is delineated in Pl. XIII, Fig. 3a. The epidermis is not widely aberrant from the normal, though the cystolith cell has been partially aborted, which was uniformly the case when these occurred over the affected mesophyll. The upper palisade layer has maintained its integrity and the lower part of the spongy layer, nearly so, for stomata are present leading into small air spaces. The central mesophyll has, it is evident, been the tissue concerned in developing the "blister." It is of some interest to note that the thickness of the blister has been attained, not by a striking difference in the number of cells, comparing the periphery with the tissue near the chamber, but by the increase in size of the hyperplasia cells, the number of cells at the periphery and near the chamber being approximately the same. The protective layer appears broken, though if the adjoining sections are taken into account, the layer is found to be continuous in the fashion of a sieve. The sharpness with which the lignified cells are delimited from the outermost layers on both sides of the leaf is a prominent fact. The smaller veins of the leaf which traverse the region affected show very little if any modification. They pass between the lower epidermis and the protective layer. They do not, however, develop sheath tissue on the upper side, the side next the sclerenchyma layer.

4. **Pachypsylla** sp. (gemma? See next). Pl. XIX, Fig. 3.

This gall is a lateral, oval swelling of the stem, generally found near or involving the nodal region. 5–7 mm. long, $2\frac{1}{2}$–$3\frac{1}{2}$ mm. wide. Color and surface texture that of the normal bark. Predominately monothalamous; confluent cases occur forming a two-chambered and even a three-chambered gall. Very common on the terminal twigs of the hackberry. Remnants of old galls can be made out on stems 5–10 years old.

The galls are commonly torn open by birds to obtain the soft insects within, which spend the winter in the galls. One of these nymphs is shown on the gall (Pl. XIX, Fig. 3).

It is not definitely known whether the imagoes from this gall and those from the next, P. gemma, are identical. The nymphs appear to be identical. The galls, however, are distinct, a difference, however, which may be referable to the plant part affected rather than to any specific behavior on the part of the insects respectively. This matter will be explained after P. gemma has been described.

This gall started in a similar manner to that of P. vesiculum, by the larva inducing a cone of tissue to grow over it, burying it in the superficial layer of the young stem. This minute cone early becomes obliterated.

A transverse section of the stem and its gall is shown in Pl. XIV, Fig. 4a. The influence of the insect in modifying the growth and differentiation of the embryonic cortical tissue, has extended nearly around the stem. The outer protective layer is much heavier and better defined than the inner. Two prominent elongate, thick plates of mechanical tissue extend from the broken inner sclerenchyma zone, outward toward the attenuate edges of the outer mechanical layer; a definite adaption to insure rigidity. The soft interior tissue bounding the larval chamber is made up of cambium-like parenchyma, the cells being very regularly oriented in radial rows. This constitutes the nutritive layer (Pl. XIV, Fig. 4c).

Fig. 4b shows in detail a part taken at b, Fig. 4a. The outermost sclerenchyma elements are true sclerides and have numerous crystal containing cells scattered among them. The cork enveloping the gall is normal, except that the number of cell layers is not as numerous as in the unaffected stem. The epidermis and often the hypodermal layer with it, is found broken and peeling off, while that on the stem opposite the gall is intact.

A much magnified detail (Fig. 4d) has been made from the region d in Fig. 4 a, Pl. XIV, to show the origin of the tissue which has formed the bulk of the gall. At this point of transition between the hyperplasia tissue and the normal, it is at once seen that the phellogen layer has furnished the meristematic tissue, which has been directed to such unusual development, for the new tissue is strikingly shown to be intercalated between the cork proper and the phelloderm, which is but one cell thick. In the region beneath the larva, the cortical parenchyma has suffered some hyperplasia, but this is not at all comparable in quantity to that of the phellogen.

In the case of the mechanical, laterally diverging plates, mentioned above, it is a matter of some interest to note that the sclerenchymatization of the two types of cells involved is perfectly uniform or continuous. While the boundary between the new cambium-like tissue and the cortical tissue proper is very definite, based upon the shape of the cells, the wall thickening processes have gone on with an equal degree of intensity in both.

5. **Pachypsylla gemma** Riley. Pl. XIV, Fig. 5.

As indicated in the specific name of the insect, this is a gall of the bud. The bud incept suffers extreme modification in its development, an irregular sub-spherical structure being formed, containing from three to eight chambers (Pl. XIV, Fig. 5). When the chambers are numerous the structure takes on a nodular aspect. 3–5 mm. long, 4–5 mm. wide. In many specimens faint outlines are present, suggesting the normal scale structure, though in no case are free scales present. The color is lighter than that of the normal buds. Very common. A normal bud is shown in Fig. 5 c, Pl. XIV.

This gall differs from the preceding in that it is uniformly polythalamous and always projects from the stem as a definite (appendicular) modification of the bud. The protective layer does not occur immediately beneath a cork layer, but differentiates beneath a thick zone of tissue, which can be interpreted as the homolog of the outer bud scale. Fundamentally, however, the two galls are similar and they eventually may be shown to be caused by the same species of psyllid. They are here separated for the reason that no transition forms between them have been observed.

In the cross section of a gall (Pl. XIV, Fig. 5 a) a heavy zone of lignified tissue is found enveloping the nutritive tissue within. The inner walls of the chambers develop somewhat irregular plate-like masses of mechanical tissue to support them. In the detail drawing (Fig. 5 b), the outer zone of homogeneous tissue is interpreted as the homolog of a bud scale. The definite row of cells on its inner border (at x) suggests epidermis. The stone-cell type of sclerenchyma forms an extremely rigid structure. The nutritive tissue does not exhibit the regular cambium-like formation as observed in the preceding gall, its elements assuming an irregular aspect; those on the inner side being tangentionally stretched. The reduced fibro-vascular bundles traverse the outer region of the nutritive layer.

6. **Pachypsylla mamma** Riley. (Pl. XIX, Fig. 9; Pl. XV, Fig. 6, 6 a).

A short, sub-cylindric gall on the under side of the leaf, 5–8 mm. high, 4½–5½ mm. wide at base, almost uniformly arising near a principal vein. The distal end varies from a definitely smaller diameter than that at the base, to a noticeably larger diameter, in the first case the galls are sub-conic with rounded ends, in the second, sub-balloon-shape, with the ends more flattened. On the upper side of the leaf is a conspicuous circular depression or basin, in the center of which a minute conic papilla is evident. This papilla is part of the first gall tissue developed, being the cone which grew up around the larva in the process of embedding it in the leaf tissue. In color the galls are light green, varying to violet and purple tints. Most specimens show a definite bluish bloom. The adult galls are smooth, though when very young they are covered with an array of long acicular trichomes. The galls when fully mature show interiorly a dome-shaped cavity, which extends to the very base of the gall. This cavity is developed through the dehiscence of the middle tissue of the nutritive layer. A secondary chamber, variable in size, though much smaller, is found in the region beneath the papilla. It represents the failure of the tissue above the larva to grow completely together. The walls are firm and brittle. The insects leave the gall about the time of the first frost and as imagoes spend the winter concealed in the bark of the tree. The galls are more or less abundant on hackberry trees everywhere.

Riley, Johnson's Universal Encyclopedia, p. 425. 1877.
Riley, 5th Rept. U. S. Ent. Comm. p. 618-619. 1890.

This histology of this gall has been previously studied by Cook (2 [v. 3, p. 426]) and Cosens (3 [p. 308]). The chief difference between those studies and the author's is the fact that the material studied for the present paper, disclosed the presence of a fine canal leading in from the distal end of the gall. This will be described in a succeeding paragraph. In the paper by Cook, the secondary chamber mentioned above was inadvertently regarded as the larval chamber.

The specimens from which serial sections were made for this study were not fully mature. The old mature galls are practically impossible to cut satisfactorily. Certain features such as the nature and development of the nutritive layer can be studied much better in a somewhat immature gall than in the old ones when that layer has been disrupted.

The gall comprises two epidermal layers, iso-diametrical parenchyma tissue, sclerenchyma (protective layer) which is particularly well developed near the dome-shaped nutritive layer forming the central region (Pl. XV, Fig. 6b).

Fig. 6d presents the details of the blind canal region outlined at d, Fig. 6b. The epidermal cells lining the canal are slightly smaller than those on the other parts of the gall. The cutin layer is continuous down the canal to its blind end at the innermost sclerenchyma zone. A group of sclerenchyma elements, relatively large and highly pitted, occur on the inner side of this zone, directly beneath the canal. Inwardly the nutritive tissue adjoining these elements is composed of exceptionally large cells which have stiffened their walls by criss-cross thickenings (Fig. 6h), a type of cell not uncommon in the larger elements of nutritive layers.

The cambium-like nutritive layer is detailed in Figs. 6c and 6e. The protective layer is well on its way in the lignification of the cell walls though it must be remembered the condition here illustrated is immature. In the fully mature galls, cells near the periphery of the cecidium become lignified and the inner cells shown in the figures finally attain walls of such thickness as to be classified as stone-cells.

The fibro-vascular bundles traverse the gall on the under side of the nutritive layer. On the side next to the nutritive layer the bundles commonly possess one layer of bundle sheath cells (Fig. 6e). The bundles collectively form a very coarse net-work over the under side of the cambium-like central tissue.

A detailed study of the cystoliths is shown at f and g, Fig. 6b, Pl. XV. These are illustrated in Figs. 6f and 6g, respectively. The one on the edge of the gall shows marked abortion, evidently possessing little calcium carbonate in its structure for it stained heavily. The other cystolith just beyond the range of the gall was entirely normal, the expanded part infiltrated with calcium carbonate staining but slightly. Houard (10, [p. 109]) reports aborted cystoliths on the border of a dipterous gall on Ficus.

Among the largest cells found in any of the galls, were some of the parenchyma units in the old, fully mature galls (Pl. XV, Fig. 6i). Contrasting with these are the normal cells of the leaf mesophyll (Fig. 6k), those of the petiole before their walls are thickened (Fig. 6m), those of the pith (Fig. 6n). All were drawn to the same scale.

The excessive enlargement of the gall cells can only go on in those cells retaining thin walls. These cells, however, cannot enlarge on the sides joining the lignified ones, hence the expansion must be at the ends away from the sclerenchyma cells. This type of development gives a characteristic radiate structure to the parenchyma locally, where it surrounds isolated sclerides or scleride groups, a condition presenting a striking appearance in the section of the old galls.

The discovery of the central, extremely narrow pit or canal in the distal half of this gall, makes it possible to correlate it to such varietal forms as Riley's P. curcurbita, which is smaller and presents a prominent, wide, yet deep, apical pit. If P. curcurbita should ultimately be shown to be a distinct species, it would as such form a transition type between P. vesiculum and P. mamma, though it stands closer to the latter than the former. One P. mamma gall studied failed to exhibit the presence of the distal pit.

7. **Pachypsylla venusta** O. S.

This gall is a large, hard, asymmetrical, pear-shaped modification of the petiole, variable in size according to the number of chambers found in the gall; the chamber number being directly related to the number of insects concerned in the formation of one gall (Pl. XIX, Fig. 8; Pl. XVI, Fig. 7). 1–2½ cm. long, 8 mm.–18 mm. wide. Surface minutely roughened, destitute of hairs. Yellowish gray to brownish in color. At one side, near the distal end of the gall is always a prominent concavity which is apt to be bordered by the remnants of the leaf blade. Interiorly, radiating from a central core, the walls give rise to conic chambers (Pl. XVI, Fig. 7a). This core, however, is attached directly to the wall of the sunken area or sinus, above mentioned. These chambers vary in number from 3 to 14. The radiating walls are very thin near the periphery where they join the hard outer shell. Fig. 7b shows the gall with the side removed. The chambers are nearly filled with a white, flocculent, waxen mass, a secretion of the nymphs. The pupæ all emerge through the thin wall of the sunken area in the fall, and after the last ecdysis the insects fly to the bark, where they spend the winter. These galls are not common, the writer's entire collection numbering but a half dozen. They have not been seen in Ohio.

Osten Sacken, B. Ent. Zeit. in Stettin. p. 422. 1861.

Before discussing the histology, it should be noted that this gall is formed in identically the same fashion as P. mamma, though there are many insects concerned in its development. Once the tiny cones of tissues, which are concerned in the embedding of all the psyllid larvæ in the petiole, have overtopped them, extensive hyperplasia takes place, this hyperplasia eventually forming the central core. The hyperplasia of the rest of the petiole (the peripheral portion) of course keeps pace with that just mentioned.

A transverse section of the gall is shown in Pl. XVI, Fig. 7c. At a, is indicated a part which is enlarged nearby. An outer and inner part of this has been drawn in detail in Figs. 7d and 7e. The first striking feature of the outer wall of the gall is that of the presence of a cork layer on it. Küster (16 [p.206]) points out that cork formation on galls is a rarity. No cork, of course is ever found on the normal petiole. The cortical parenchyma cells have not thickened their walls as those of the normal petiole do. An extremely heavy layer of stone cells is developed, but is not continuous; numerous strands of parenchyma tissue extend through it. The nutritive layer (Fig. 7e) consists of the same thin walled type of tissue seen in that of the other galls, but it does not possess, in the adult condition, the typical cambium-like structure. The fibro-vascular bundles located in the outer part of the nutritive layer are small and numerous (much more so than indicated in the diagram). No bundle sheath is developed.

The central core is composed of a homogeneous mass of very large sclerenchyma cells. One of these is figured, Fig. 7f. The simple pits in the wall extend as far as the middle lamella. Fibro-vascular tissue is entirely absent from the core, a fact related to the origin of the structure, for the embryonic tissue concerned in its development never was related to the procambial strands, but was entirely new hyperplasia tissue. The pores leading from the chambers through the core are lined with short multi-cellular trichomes. (Fig. 7g).

Fam. ITONIDIDÆ (Ord. Diptera).

This family, formerly known as the Cecidomyiidæ, embraces a large assemblage of gall makers. In the vast majority of cases, the egg is deposited superficially on the very young plant parts. The gall does not begin development until the larva hatches out and places itself in intimate contact with the embryonic plant tissue. This is followed in the galls found on the hackberry, by an upward growth of the tissue about the larva. The tissue above the larva never completely grows together, leaving what is called in the present paper an "apical canal." This very common type of gall is called by Küster the "umwallungen" form, a word very satisfactorily expressing the real nature of the gall. This type of cecidium stands in marked contrast to that in which the larva sinks into a diverticulum or pouch, a kind found on the leaf blade only.

Of the nine galls set forth in this paper, only three have had the adult insects associated with them described and named. Patton (26) in order to illustrate a method of naming galls, gave specific names to a few of the following galls, which Riley (28) had described, but properly left unnamed. Riley did not have the adult insects and Patton did not see Riley's galls, so we have the interesting case of a gall insect being named without the writer having seen either the gall or the insect. These names of Patton's are omitted from the present paper.

The galls described for the first time in this paper, are given a list number, which can be referred to by the entomologist who finally describes the adult insect. The heretofore undescribed galls and those yet unnamed are placed provisionally under the old genus name Cecidomyia, which has long served as a "storage" place for itonid "insectæ imperfectæ".

All of the galls are not worked out to the same degree of detail since they are of fundamentally different structure. Two of the simpler forms, exhibiting contrasting specific characters, have been chosen to adequately present, by full treatment, the histology of the itonid types on the hackberry.

The author, at this point, wishes to express his deep appreciation of the kindness of Dr. E. P. Felt, State Entomologist of New York, the American authority on the Itonididæ, for many helpful suggestions pertaining to the identity of some of the gall forms herewith presented.

Riley (28) describes one gall which has not been collected by the writer. To give a character of completeness to the itonid list, his data on this form will be given.

"33. On the under side of the leaf, arising from the leaf ribs, occurring either singly or in smaller or larger groups. Gall rosette-shaped, resembling the seed capsule of certain Malvaceous plants of the genus Hibiscus, circular in outline, greatly flattened on top and here furnished with a short central spine or nipple (frequently broken off); sides sulcate, with from ten to twelve more or less marked furrows, and with the corresponding interstices convex. Surface of gall not shining, lighter or darker brown, speckled with small, irregular, blackish pustules, and sparsely beset with moderately long whitish hairs, which are easily abraded. Average height of gall, .75 mm.; diameter 2–3 mm. Cell oblong oval, enclosed by thick, woody side walls, but with a thin bottom, and at the roof (i. e. toward the upper side of the leaf) covered with a thin soft layer. The gall is at once recognizable from its shape, but might readily be mistaken for a Psyllid gall" Riley.

This gall is probably Cecidomyia "lituus" Walsh, which is given by Felt as a "yellowish, disk-shaped gall with acute apical cone on leaf." Walsh's name "lituus" should not be associated with any hackberry gall. In the citation below he gave this name to the grape gall now called C. viticola, and mentioned, merely, the presence of two "similar galls" on hackberry leaves.

Walsh, Am. Ent. 2:28. 1869.
Riley, 5th Rept. U. S. Ent. Comm. p. 613. 1890.
Felt, Jour. Econ. Ent. 4. 1911.

8. **Cecidomyia unguicola** Beut. (Pl. XVII, Figs. 8, 8a).

On leaf, under side, a, sharply pointed cone-shaped gall with flaring base. 3–5 mm. high, 2–3 mm. wide. Light green to yellow in color. Smooth, almost shining. Monothalamous, rarely, if ever confluent. Chamber sub-cylindric, with the distal half thinner walled than the proximal. The distal one-third or one-fourth of the gall is delimited proximally by the sudden transition from delicate sub-hyaline tissue to opaque hard tissue. Sooner or later the tip breaks off at this point. Riley states that "while issuing the perfect insect pushes off the tip." This gall is the most common of all the itonid galls of the hackberry; a hundred may often be found upon a single leaf.

Riley, 5th Rept. U. S. Ent. Comm. Gall No. 34, p. 614. 1890.
Beutenmuller, Bull. Am. Mus. Nat. Hist. 23:388, Pl. 13, Fig. 9. 1907.

The entire longitudinal section of this gall is illustrated in detail in Pl. XVII, Fig. 8a. This figure and the next are slightly diagrammatic in that the fibro-vascular bundles, which traverse the gall longitudinally without branching, are shown continuous, when actually they would be broken in any one of the serial sections, due to the fact that they do not pass to the tip of the gall in one plane.

The epidermis is uniformly composed of simple tangentionally flattened cells. The nutritive and protective layers assume an elongate cup shape, whose base is surrounded by the parenchyma tissue, which gives the gall base its flaring aspect. The nutritive layer is very thin, seldom over three cells in thickness. Note the unbroken condition of its superficial cells. The larvæ in all of the galls of this type do not feed on the cell tissues, but on the food material which passes into the chamber through the cell walls. The protective layer is sharply delimited from the nutritive, a condition common to all of the itonid galls studied. On its outer side the protective layer is only sharply set apart from the parenchyma on the side toward the leaf.

The nature of the cells composing the protective layer is shown in Fig. 8d, a small group of cells at the proximal end of the layer. The walls contain innumerable simple narrow pits, which pass to the middle lamella. This latter structure is in all cases continuous between the cells. Crystal cells are found in abundance directly adjoining the lignified thick walled cells, a condition obtaining in the normal stem (Pl. XII, Fig. A). Figs. 8e and 8f show the sclerides of the 1 yr. and 3 yr. old stems respectively, and are drawn to the same scale as those from the gall. The great majority of the lignified cells of the galls are larger than any found in the stem or in the stone of the fruit.

The distal one-third of the gall is composed of rows of very thin walled cylindrical cells. Distally the inner superficial layer of these give rise to numerous coarse trichomes, which choke the apical canal leading to the larval chamber.

The fibro-vascular bundles are not as large in proportion to the rest of the tissues as the principal bundles of the leaf. Their number and distribution are shown in Fig. 8b. Basally they are related directly to the bundles of the leaf or as is often the case they form a "knot" in the median basal region, this "knot" being related to a number of leaf veins. Küstenmacher (14) finds a similar "knotted" condition of the bundles at the base of certain Rhodites galls. The xylem elements are fine spirally thickened tracheids. The phloem cells are simple elongate cells whose end walls slant at a more or less prominent angle. No bundle sheath tissue is evident; the proximity of the bundles to the rigid protective layer making possible their support without the normal mechanical tissue being present.

The normal leaf (Fig. 8a) is very little affected where the gall is attached to it. The epidermis with its cystoliths and two palisade layers, exhibits hypertrophy, but this not to a marked degree. It is evident that the primordium of the spongy layer has furnished the basis for the hyperplasia constituting the gall.

In the chamber region is shown the section of the larva.

9. **Phytophaga celtiphyllia** Felt. (?) Pl. XVIII, Figs. 9, 9a.

A sub-balloon-shaped gall occurring on the leaves (either side), petioles and stems. 4–8 mm. high, including the apical, variable, attentuate tip, which arises sharply from the distal end of the gall body. 4–5½ mm. dia. through the broad distal half of the gall. The sides do not taper proximally in the typical balloon fashion, but show a definite constriction below the distal expanded portion. When isolated the galls show a perfect radially symmetric structure, but they are apt to be found in clusters, resulting in more or less loss of symmetry through mutual pressure. When on the leaves they generally are found on the upper side attached close to the principal veins. These galls retain their green color longer than any of the others; when full size in mid-summer, the content of chloroplasts in the superficial cell layers is so great as to make them fully as green as the leaf. Coarsely pubescent. The chamber is constricted distally. Galls not uncommon in Kansas, but this form has not been seen in Ohio.

The writer is practically certain that this is the gall described by Pergande, whose notes are presented by Felt with the description of the above insect. Pergande states it to be a "very hard, obconic gall, the upper extremity produced as a long slender nipple; at the base five or six low ridges. The galls occur on the upper side of the leaf and drop when mature." Unfortunately no measurements are given. On the basis of the brief description, however, absolute certainty is not possible.

Felt, N. Y. State Mus. Bull. 180, p. 216. 1914.

The histology of this form, (Pl. XVIII, Fig. 9a), while fundamentally similar to that of C. unguicola, just described, presents many points which are of particular interest when contrasted with the features of the other gall.

A specimen on the leaf was chosen so that the two galls can be said to have a similar origin. The distal expanded or flaring portion of this gall (8) is seen to be due to the development of a mass of large celled parenchyma, comparable to that found in the proximal part of 7. The protective layer is thicker and divides distally so as to form a definite support for the mass of parenchyma just mentioned. The nutritive layer is extremely well developed; the thickest of any of the itonid galls. It will be noted that it is intact. The apical canal of the gall is not continuous into the chamber, the walls at its inner end having become tightly pressed together. The line between the two epidermises, however, was easily found in the serial sections used. The outer part, of definite diameter, is choked with slender trichomes, which are certain of the epidermal cells greatly elongated. The fibro-vascular bundles traverse the protective layer. Much more of the leaf is involved in this gall than in number 7 (Fig. 9a). In that portion of the leaf involved, the usual inhibition of the normal differentiation has ensued, the hyperplasia consisting of little more than a mass of parenchyma bearing greatly hypertrophied epidermal cells (gall trichomes) and the vascular tissue. As in all of these galls, no cystoliths or stomata ever were seen associated with the hyperplasia tissue. The longitudinal section of the larva is indicated in the chamber.

Fig. 9b shows the detail of the region indicated at Fig. 9a, b. The simple-pitted sclerenchyma cells differ only in the shape they have assumed on either side of the vascular bundle. On their outer side they are bordered by crystal "sacs," a relation which as observed earlier, obtains in the normal stem. More highly magnified sections of these cells are shown in Pl. XVII, Fig. 9c.

10. **Phytophaga wellsi** Felt. Cecidium nov. (Pl. XVII, Figs. 10, 10a).

On leaf, under side, more or less definitely obconic, resembling the shape of a somewhat flattened top. Generally found in clusters attached to the sides of the principal veins near the point of their divergence from the petiole. 2½–3 mm. high, 3–4 mm. wide. Distal end shows a more or less definite central prominence. Yellowish tinged, with short pubescence. Walls pithy in texture, yet firm; tissue when old, brown. Chamber sub-cylindric. Protective layer poorly developed, confined to proximal one-third of gall. Nutritive layer very thin. Fibro-vascular bundles traverse galls near the surface. This is the simplest of all the itonid galls studied.

Description of adult insect by Dr. E. P. Felt, in manuscript.

11. **Cecidomyia** sp. (Pl. XVII, Figs. 11, 11a).

On leaf, under side, a small (2–3 mm. long, 1–1½ mm. wide) sub-cylindric gall with attenuate tip, which is more or less definitely constricted from the body of the gall. Base rounded, light green to yellow, smooth. Thin walled, the chamber approximating the shape of the gall. The galls are commonly tilted over at a sharp angle, particularly when they arise from one of the larger veins. The protective and nutritive layers are distributed much as those of No. 7.

Riley first described this gall (No. 35 in his paper) and called attention to its similarity to C. unguicola Beut. (See No. 8). It differs constantly from that gall, however, in its smaller size and its non-flaring base.

Riley, 5th Rept. U. S. Ent. Comm. p. 614. 1890.

12. **Cecidomyia** sp. (Pl. XVII, Figs. 12, 12a).

"On leaf, under side, stoutly conical and nippled at tip. Succulent, pale green, and covered with fine bloom when young. 3x4 mm. Present in great numbers; larva, white." Sears.

The author's specimens rarely go over 3 mm. in high. They vary from 2–3 mm. in width. Many are purplish tinged. The chamber is sub-cylindric, rounded below.

The protective layer is well developed and extends distally as far as the inner opening of the apical canal. The nutritive layer is confined to the proximal half of the chamber wall. The fibro-vascular bundles pass upward close to the protective layer.

Sears, Ohio Nat. 15:384. Pl. 19, Fig. 33, 1914.

13. **Cecidomyia** sp. (Pl. XVII, Figs. 13, 13a).

"Leaf gall, present in great numbers on under side. A "peg-shaped" gall, cylindrical when young, and developing a thickened base as it grows. Pale green, straggling hirsute, 2–3 mm. long. Very common." Sears.

The broad, ill-defined ridges which characterize the base of this gall separates it from all others. The protective layer is relatively thick, but does not extend into the wall of the distal end. The nutritive layer is thin. The fibro-vascular bundles pass through the parenchyma basally but approach the protective layer apically.

Young specimens of this gall would closely approximate the gall described in Riley's report under No. 30. The expanded condition of the base is not gained until the gall has nearly completed its growth in length.

Riley, 5th Rept. U. S. Ent., Comm. p. 612. 1890.
Sears, Ohio Nat. 15:384. Pl. 19, Fig. 35. 1914.

14. **Cecidomyia** sp. (Pl. XVIII, Figs. 14, 14a).

A large, globular, mucronate tipped gall of the stem. 5–8 mm. dia. Base varies toward a truncate condition in some specimens. Green throughout the summer; finely pubescent. Chamber large, spherical. A thin membrane is constructed by the larva across the distal end of the chamber. Protective layer thick, nearly half as thick as the wall. Does not extend to apical canal. Nutritive layer relatively thin. The fibro-vascular bundles traverse the protective layer.

Riley describes a globular gall, which on "detaching the gall, the base is seen to be truncate and attached to the rib of the leaf by an extremely short, conical style, which is not visible from the sides. Average height, 3.5 mm., dia. at middle, 3.5–4 mm." See No. 32 in Riley's list. This gall might be interpreted as an immature specimen of the above. Sear's number 34 is a variation of the above with the basal one-third developing low irregular ridges.

Riley, 5th Rept. U. S. Ent. Comm. p. 613. 1890.
Sears, Ohio Nat. 15:384, Pl. 19, Fig. 34. 1914.

15. **Cecidomyia** sp. (Pl. XVII, Figs. 15, 15a, 15b.)

This gall exhibits a remarkable variation from the previously described simpler types. Riley, who first described it, gave a very complete description of it, which will be quoted.

"31. Galls on the tender twigs, occurring either singly or in groups of two, three or four or more specimens; rarely also singly on the under side or even the upper side of the leaf. The gall bears a close resemblance to the winged seed capsule (achenium) of a Rumex, but the wings vary in number from three to five and are often irregularly developed, while the tip always ends in a curved, long spine. The wings terminate in a sharp ridge which is sometimes double. Gall opaque, not hairy. Color pale-yellowish green, at apical third usually of a more decided green and darker. A longitudinal section reveals a single large regularly ovoid cell surrounded by a thin hard wall. Average height of gall, 4.5 mm., excluding the apical spine; generally as wide as high; length of apical spine variable, but usually a little more than half the height of the gall." Riley.

The histology presents some points of special interest. The fibro-vascular bundles are found in the edge of the wings (Pl. XVII, Fig. 15b), from which branches are distributed inwardly to the protective layer. This is better shown in the longitudinal section, Fig. 15a. The protective layer is found, as in most of the preceding galls, to be confined to the proximal two-thirds or three-fourths of the chamber wall. Trichomes line the apical canal to the point where it opens in the chamber.

16. **Cecidomyia** sp. Cecidium nov. (Pl. XVIII, Figs. 6, pl. XIX; 16, 16a).

A gall of the leaves, stem, petiole or fruit occurring generally in an aggregate condition. An isolated specimen on the stem will be described to elucidate the fundamental unit characteristics (Pl. XVIII, Figs. 16, 16a). When found singly, the gall is irregularly conic or sub-cylindric, with a very blunt truncate tip. The chief character is involved in the fact that the gall eventually drops its larval chamber enclosed by the nutritive and protective layers. This central part of the gall which slips out has the shape of a short, blunt horn. The tapering of this structure toward the proximal part of the gall makes possible the easy departure of this larva containing portion when the dehiscence layer surrounding it gives way. The gall aggregates commonly occur at or near the end of the stem, the tissue, after the larval chambers have fallen, dying, turning black, giving the twig an unsightly appearance (Pl. XIX, Fig.6). In the case of a single gall (Pl. XIX, Fig. 4) the stem is not killed, but the tissue of the "socket" part is cut off by an abscission layer (Fig. 16a, Pl. XVIII).

The gall on the fruit (Pl. XIX, Fig. 8) possesses exactly the same structure as those on other parts of the plant. The galls shown are not mature, the chamber not having burst through the surrounding supporting tissue. In section (Pl. XIX Fig. 4) the galls are seen to project into the ovulary cavity, exhibiting in their entirety the characteristic shape observed in those of the leaf which project from both sides of the leaf. The ovule is aborted.

The most important histological feature is naturally associated with the chief feature of the gall and consists of the dehiscence layer developed around the protective layer. This layer (Pl. XVIII, Fig. 16a) is made up of extremely thin walled cells, arranged in rows, radiating from the protective layer. It gives evidence of having been formed by rapid division when the gall was nearing maturity and becomes intercalated between the fibro-vascular system and the protective layer. Its eventual disintegration separates it cleanly from the protective layer, leaving the central part containing the larva free to be shaken out by the wind.

A few similar types of galls are known among the Cynipidæ and Itonididæ. Houard (11) figures an itonid (Oligotrophus Reaumurianus Loew) which is exactly similar. It occurs on Tilia grandifolia of Europe.

Comparative Studies.

Kataplasmas.

The two kataplasmas (galls 1 and 2) possess differences related in part to the position of the parasites on the stem. The excessive hyperplasia of the cortex, in the case of the witches-broom branch bases, seems to be associated with the superficial position of the mites, while in the case of the lepidopterous gall the greatest hyperplasia is that of the pith, the medullary rays and cambium region, a condition correlated with the internal position of the larva.

Suppression of normal differentiation characterizes both. The lepidopterous gall partially developes bast, but no sclerides appear. The mite gall exhibits sclerides, but no bast. No lignification of the undifferentiated xylem cells occurs in the lepidopterous gall, but is very definitely found in the acarinous cecidium.

Compared with the normal stem, the most significant single fact concerning the kataplasmas, is the marked inhibition of differentiation with no substitution of entirely new tissue forms.

Prosoplasmas. Hemipterous galls.

Pachypsylla vesiculum (gall 3 and Fig. 3) is the simplest of the psyllid galls. Compared with the normal leaf it would appear that the middle cells of the immature mesophyll are most susceptible to the influence of the nymph, since these cells have carried out the hyperplasia.

The other four galls are all fundamentally identical in structure and mode of development with that of P. vesiculum. Gall 4 is the abnormally differentiated bud primordium. Gall. 5, (P. gemma) has developed for the most part from the stem phellogen, a tissue in the young stem undoubtedly more susceptible to control than that of the cortex. Gall. 6 (P. mamma) involves all of the leaf tissues, so that the gall can be considered as a mass of "new" tissue intercalated in the leaf blade, but suspended below the leaf blade plane. Gall 7 (P. venusta) illustrates the same mode of development seen in No. 6, carried out on the petiole by a number of larvæ rather than one. (See description under 7).

It can be said that the above psyllid galls, characterized by little or no "umwallungen" development with rather ill-defined protective layers surrounding nutritive tissue possessing a cambium-like structure, constitute a generic type of gall for the hackberry, a type which contrasts strikingly with the generic type of itonid galls.

It is of course evident that the specificity of the different galls is in part due to the instinctive behavior of the insects in choosing particular plant parts. This is strikingly shown by comparing P. mamma with the gall on the side of stem (No. 4).

The evagination beneath the larva so prominent in the case of P. mamma could not, naturally be carried out on the stem, hence the hyperplasia in that case is almost entirely lateral to the insect and above it. Discounting the factor of the plant part selected there is the quantitative evidence indicating specificity in the intensity of the stimulus which developes the generic type of gall.

Compared with the normal tissues these galls show the abortion or complete absence of certain normal specialized cells, such as stomata, cystoliths, tracheæ, bast, wood fibres and sieve tubes.

Prosoplasmas. Dipterous galls. (Itonididæ).

Galls of Cecidomyia unguicola (8) and Phytophaga celtiphylla (9) were chosen to illustrate in detail the definite specificity which characterizes these highly evolved forms of prosoplasmas, which are induced by the insect larva to grow upon the same leaf. This fact of the gall species being definitely and constantly related to the insect species, is a fact of far reaching significance. It has long been known among European workers and Cook (2) on a histological basis, first called attention to it in America.

In the case of these two galls some of the contrasting characters are: Notable difference in size (they are drawn to same scale). In 8 the proximal development of large celled parenchyma, opposed to its distal development in 9. Much thicker protective and nutritive layers in 9 than in 8; shape of layers also different. Apical canal tightly closed proximally in 9, open throughout in 8. Trichomes in apical canal of 9 smaller than those in canal of 8. Large acicular trichomes developing over surface of 9, while 8 is always perfectly smooth. Hyperplasia of leaf at base of gall, extends much farther in 9 than 8.

Comparing the other itonid galls in a similar manner will yield just as striking results. In the following discussion of the remainder of the galls, only the more significant specific characters will be emphasized.

Phytophaga wellsi (10) is the least specialized. Its protective layer merging insensibly into the distal parenchyma and its simple closed apical canal are the two most important characters placing it below the others in the degree of complexity attained.

No. 11 is similar to 8, but simpler. It is constantly smaller and does not develope the expanded base, so characteristic of 8.

The extension of the protective layer to the apical canal is found in No. 12 only.

In No. 13, the epidermis lining the chamber at the apical end of the gall is composed of perpendicularly elongated cells which are filled with a fine granular substance (Fig. 13b, at x, pl. XVII), the nature of which was not determined. The character was constant, being exhibited in many galls examined. Such a cell layer was not observed in any other itonid gall.

No. 14 has the fibro-vascular bundles traversing its sharply defined protective layer. In this respect it is similar to 9. These two galls differ from all the others, having definite protective layers, in this character. Küstenmacher (14) has noted the diversity in Rhodites galls in this regard.

The alate condition of 15 makes it an object instantly indentifiable. With this character is associated the peculiar distribution of the bundles (Fig. 15a, pl. XVII), not found in any other gall.

No. 16 possesses many characters setting it apart from the others, the most important of which is the development of the dehiscence layer in it, permitting the larval chamber to drop out. Nothing in any of the other galls is directly comparable to it.

All of the hackberry itonid galls are of the "umwallungen" generic type. The kinds of cells found in the galls are not widely dissimilar, the specific characters being confined to the kinds of tissues, with particular reference to the form the tissues assume.

There is a character which the writer desires to point out, which is found not only on most of the itonid galls of the hackberry, but on those of other plants, the significance of which has not been determined so far as the author is aware. The protective layer in most of these galls is sharply delimited apically giving rise to a distal segment of the gall composed wholly of parenchyma (No. 12 excepted) a segment which is evident in many galls upon superficial examination.

It is proposed to call this segment the "apical segment," though the writer has not used this terminology in the present paper because of the uncertainty as to its value in taxonomic description. No ontogenetical studies of this type of gall have as yet been made by the writer to demonstrate if this apical segment bears any relation to the minute cone which early developes over the newly hatched larva.

In way of summary it can be stated that the hackberry itonid galls exhibit in an especially strong fashion, specificity, based upon the generic "umwallungen" type of cecidium. This specificity is directly related to the specific physiological phenomena of the larva and holds, whether the gall appears on the young tissues of the leaf, petiole, stem or fruit. The insects commonly, however, tend to oviposit on a particular plant part, (this probably being the most important factor in determining the position the larva eventually takes), and the galls thus become associated with that part. But as in the case of 16, it is seen that the character of the gall's position on the plant would be of no taxonomic value whatever, since these galls have developed from the young tissue of leaf, petiole, stem and fruit. Many of the others have been reported from more than one plant part.

The comparison of the two generic types of prosoplasmatic galls will yield some interesting data.

Of the psyllid galls Pachypsylla mamma (6) shows best the generic type to which it belongs. Occurring on the leaf it can be contrasted to advantage with the numerous itonid leaf galls. Given the P. mamma larva and an itonid larva (one like Nos. 9 or 13, which commonly form galls on the upper side) on the same young leaf, on the upper side there will occur an entirely different series of changes as evidenced in the final stages, the mature galls. In the case of the psyllid the minute "cover" cone which grows up around the larva, remains small, the gall being composed almost wholly of hyperplasia tissue beneath and to the sides of the larva. The larva is lowered, as it were, in a downward evagination, the sides of which growing inward above eventually developing a thick wall over the larva. The primal "cover" cone does not contribute to this, but remains small and can always be seen in the center of the upper concave side of the gall as a minute papilla.

In the itonid gall very little hyperplasia takes place beneath the larva, the gall being developed from the primal "cover" cone, the gall becoming an appendicular structure on the upper side of the leaf, while in the psyllid it is on the under. Most of the itonid larvæ begin operations on the under side of the leaf, resulting in the gall having that position, but this does not destroy the significance of the fundamental difference between the two types of galls.

Histologically the itonid galls show a much higher condition in the definiteness with which the nutritive, protective and parenchyma tissues are distributed. Also, greater diversity of specific characters is introduced by the larvæ, in itonids than in psyllids for in the latter a definite part of the form character is related to the kind of plant part on which the gall is developed. In the itonids the form character is wholly related to the larva.

Comparing the prosoplasmas with the normal tissues it is strikingly evident that we have, as many European cecidologists have pointed out, entirely new structures. This "newness," however, in the hackberry prosoplasmas, consists of new forms, assumed by tissues, which are composed of cells that have close if not identical counterparts in the normal parts. Commonly the parenchyma and sclerenchyma elements of the gall tissues are much larger than those found in the unaffected structures, but in no case can it be said that the cells of the galls are fundamentally different from those observable in the normal plant.

Heteroplasmas, (All of the galls).

In comparing the kataplasmas with the prosoplasmas, it can be inferred that the amount of embryonic tissue influenced in the beginning stages of the gall is greater in the former than in the latter. In the case of the lepidopterous gall the fact of the greater range of the stimulus is doubtless associated with the relatively greater size of the larva; in the mite gall, to the numerous individuals present at a particular point of attack. In both cases this condition is enhanced by the migration of the arthropods from one part of the affected region to another, a phenomenon known to take place in these galls, but which is not true of the prosoplasmas. In these the larva is quiescent, while the definite new form of tissue is growing about it. This has been demonstrated by the writer in P. mamma and by Fockeu in dipterous galls. The low type of heteroplasia (kataplasma) relatively undifferentiated, and the highly differentiated form (prosoplasma) undoubtedly owe their difference in great part to the distinction in the arthropods just pointed out.

It should be noted that the difference between kataplasmas and prosoplasmas is not a difference in kind, but a difference in degree only, as Küster (15) pointed out when first presenting this terminology.

The xylem of the kataplasmas showed the presence of subnormal tracheæ, while that of the prosoplasmas, even though occurring on vessel bearing parts, always possessed narrow, elongate, spirally thickened tracheids only.

All of the galls when compared with normal parts show partial or total suppression of normal tissue characters and the substitution of new characters. The new characters, no matter whether little or greatly divergent from the normal, are specifically related to the arthropod concerned in calling them forth.

In all of the galls, except the lepidopterous one (2), lignification of certain parenchyma elements has taken place, giving rise to more or less definite sclerenchyma tissue forms (protective layers), which in no case finds a counterpart in the normal plant. This layer doubtless is definitely functional in preventing mechanical injury to the larva.

General Considerations.

This paper does not deal directly with the etiological problem, the greatest problem in cecidology, but does deal with it indirectly in attempting to make clearly evident, the phenomena appearing at the end of certain gall ontogenies; the phenomena to be explained (it is hoped) through etiological investigations. At this point it might be well to state (for it is a fact not generally known) that the nature of the stimulus applied by the insect is not known. Magnus (20), whose recent work presents an excellent summary of the etiological problem, closes with this sentence: "Der hypothesen sind genug gewechselt, lasst uns auch endlich Tatsachen sehen." All the evidence arising out of experimental studies of the problem point toward a chemical interpretation (enzymes, etc., secreted by the larva), but as Küster (17) repeatedly has pointed out, the experimental evidence definitely supporting any chemical interpretation does not yet exist. In the true scientific spirit he acknowledges the chemical theory to be, as yet, a necessary inference only.

From the preceding comparative studies, particularly those of the prosoplasmas, it is clearly evident that the gall represents something new as far as the *form* content of the tissues and their particular orientation is concerned. The particular combination of sclerenchyma form, parenchyma form, and bundle tissue, observable in any of the prosoplasmas, does not even find an analogy in the normal structure. The cells of the galls, however, all have their homologs in the normal tissues. Cosens (3) states: "The conventional view to account for these phenomena is that the protoplasm has been endowed with entirely new characteristics and power to produce something foreign to the normal host. But this probably is true only in a very limited sense for according to my experience at least the prototypes of such apparently new tissues, etc., have been found elsewhere in the host or its relatives." He bases this statement on a comparative study of special structures, such as "glands, trichomes and aeriferous tissue," which reappear in certain galls in *addition* to the definitely new tissue "forms," constituting the gall as a whole. Any comparative studies of cecidia and normal parts should take into consideration the whole structure and when this is done the essential "newness" of the cecidium appears.

In the form characters of the gall tissues (gained through growth, i. e., proliferation and differentiation of cells) we have characters, which without any doubt whatever, are ascribable to the specific physiological phenomena of the insect. In other words the insect larva controls the growth of the embryonic tissue in its immediate vicinity, this growth developing a new structure, showing specific characters as definite and constant as the group of characters observable in the adult insects. A glance at plates 6 and 7, showing nine species of itonid galls, all but one of which have been seen by the author, on Celtis leaves, will demonstrate to any one the validity of the above statement.

An analysis of form character can be made, which will disclose certain factors over which the insect has undoubted control.

Form character with respect to tissues in the normal plant is directly related to the orientation of the mitotic spindle axes and the number of divisions during growth, and the sizes attained by the cells after mitotic activity has ceased. These factors are of course influenced by the ever present factor of environment. To the growth factors should be added the factor (the nature of which is unknown) which directs differentiation. In the gall problem this is particularly involved in the appearance of the lignified sclerenchyma tissue (protective layer), which in all cases represents a zone of parenchyma cells, which change their activity from growth to thickening of their walls.

In the case of the development of a number of species of galls on a particular leaf, the physical environmental factor can be thrown out, since it is the same for all. It is the biological environmental factor (the larva) which is now the external factor controlling the internal ones operative in developing tissues. These internal ones, to state them again are: The factor or factors related to the orientation of mitotic spindle axes and the number of mitoses carried out; the sizes attained by cells after mitotic activity has ceased; the factor or factors directing the distribution of differentiation products, which in this morphological study has particular reference to the thickening (lignification) of walls. Any theory concerning the nature of the stimulus should adequately explain how the particular stimulus exercises its control over the above factors, which factors, be it noted, are the most important factors entering into the growth of tissues.

It should be noted in the above analysis care has been taken to definitely distinguish between the factors related to the development of particular kinds of tissues and those related to the development of particular kinds of cells. These distinctly intra-cellular factors making possible mitosis, growth in size of cell, lignification of cell wall and the like, it would appear are practically undisturbed, for from the standpoint of the cells there is little or no fundamental difference between those simpler ones in host tissue and those in the galls. It should be remembered, however, in this connection, that highly specialized cells, such as cystoliths, etc., do not appear in galls.

Before leaving this phase of the subject, attention should be called to the fact that much evidence exists to show that these fundamentally new gall tissues are carrying out fundamentally new functions. This material, however, would be out of place in a paper intended to be purely morphological.

Material of some interest may be forthcoming if we view the above conclusions in the light of modern genetic conceptions.

Cosens (3) states, "this much is certain that there appears to be an entire lack of evidence supporting the view that the protoplasm of the host has become endowed with a property that enables it to produce a fairly definitely shaped but withal abnormal structure. Such a pronounced change would surely be expressed in the heredity characteristics, yet there is not a vestige of proof tending to show that insect galls ever produce the slightest variation in the descendants of the host." The "protoplasm" referred to above is the germ plasm and, used in this sense the statement made, is correct. While nothing is known concerning the difference in the meristematic tissues of gall bearing plants as opposed to non-gall bearing forms, there is no reason for hypothesizing a special constitution for the germ plasm of the gall bearing flora. Nearly all of the orders of the Anthophyta possess gall bearing plants.

On the contrary, morphogenetical studies constantly and definitely point to the germ plasm of the insect as the place of origin of gall forms. These gall forms (tissue forms taken collectively) are almost without exception found to be specifically related to the insects associated with them, this being exhibited in the most striking manner in all of the higher prosoplasmas. In the prosoplasmas it can, with certainty, be said that we have the remarkable and unique case of the overlapping, as it were, of an animal hereditary constitution on that of a plant; a situation in which the plant's tissue "forming" factors (not tissue growing factors) are suppressed and new ones substituted. In this connection it should be remembered that in the early stages of all prosoplasma ontogenies, the larval insect is in contact with the undifferentiated plant tissue; a contact as intimate as that between one part of a growing plant and an adjoining part. Fockeu (6) correctly states that the early phenomena observed in the reaction of the plant part is "en rapport" with the "phenomenes vitaux" of the gall inducing form.

Since science knows little or nothing concerning the mechanism by which hereditary factors are enabled to come to expression in form and otherwise, it is suggested that in the zoocecidological field, we have a unique place to attack this problem. Hybridization of gall insects to see if the F_1 and succeeding generations of galls would follow known hereditary laws, undoubtedly would prove an extremely suggestive line of investigation. But the great discovery which will undoubtedly go far toward helping us understand the mechanism of heredity will be that of the exact nature of the stimulus involved in producing these problematic plant tissue **forms,** comprising the prosoplasmatic zoocecidia.

Summary.

1. There are seventeen known species of zoocecidia occurring on Celtis occidentalis, belonging to four orders of arthropods: Acarinæ 1, Lepidoptera 1, Hemiptera 5, Diptera 10. All are heteroplasias, i. e., those forms of hyperplasias (abnormal increase in size through cell proliferation) whose cells and tissues differ from the normal. All, be it noted, are built up on the basis of the same germ plasm, viz., that of the single species of the plant mentioned.

2. The acarinous and lepidopterous galls are kataplasmas, or those forms of heteroplasias whose cells and tissues do not vary widely from the normal. Each shows specific and characteristic inhibition of differentiation.

3. The hemipterous and dipterous galls are prosoplasmas or those forms of heteroplasias whose cells and particularly whose tissue forms differ fundamentally from those of the normal parts. Each of these galls shows definite specificity. In the hemipterous forms the specific characters are in part related to the plant structure which bears the gall; in the dipterous galls the specific characters are wholly related to the specificity of the physiological phenomena associated with the species of larvæ concerned in the development of the galls.

4. In the prosoplasmas the types of cells found are closely comparable to those of the normal plant parts, but the tissue **forms** discovered are fundamentally new; no analogous structure forms are to be found in the tissues of the normal plant or its allies.

5. In the dipterous prosoplasmas, since the gall's specific tissue **form** characters are related to the species of insect, we have the unique case of the "overlapping" of the hereditary constitution of an animal on that of a plant in the sense that factors associated with the insect determine the form character locally, rather than those normally associated with the plant's germ plasm. These latter plant factors suffer suppression.

6. It is suggested that in the field of zoocecidology we probably have a unique place, heretofore unrecognized, to attack the problem pertaining to the mechanism used in the expression of hereditary characters.

LITERATURE.

(Only the more important literature consulted is presented here.)

1. **Abromeit, J.** Syringa vulgaris mit Hexenbesenbildung. Jahresber. d. Preuss. botan. Vereins zu Konigsberg i. Pr. 1900–1901. p. 53.
2. **Cook, M. T.** Galls and Insects Producing Them. Ohio Nat. 2:263–278. 4 pls. 1902; 3:419–436, 6 pls., 1903; 4:115–147, 4 pls., 1904.
3. **Cosens, A.** Morphology and Biology of Insect Galls. Trans. Can. Instit. 9:297–387, 13 pls., 1912.
4. **Crawford, D. L.** A Monograph of the Jumping Plant-lice or Psyllidae of the New World. U. S. Nat. Mus. Bull. 85. 1914.
5. **Felt, E. P.** Host and Galls of American Gall Midges. Jour. Econ. Ent. 4:451–475. 1911.
6. **Fockeu, H.** Recherches anatomiques sur les Galles. Etude de Dipterocecidies et Acarocecidies. 162 pp., 12 pls. Le Bigot Freres. Paris. 1896.
7. ——— Contributions a l'Histoire des Galles. Etude anatomiques de quelque especes. Camille Robbe, Lille. 1889.
8. **Houard, C.** Recherches anatomiques sur les Galles des Tiges: Pleurocecidies. Bull. scientif. de la France et de la Belgique. 38:140–419. 1903.
9. ——— Recherches anatomiques sur les Galles des Tiges: Acarocecidies. Ann. d. Sc. nat. Bot. 20: 289. 1904.
10. ——— Les Galles de l'Afrique occidentale francais, II. Marcellia 4:106–112, 10 figs., 1905.
11. ——— Les Zoocecidies des Plantes d'Europe et du Bassin de la Mediterranee. 2 tomes. Paris. 1909.
12. **Kellerman, W. A.,** and **Swingle, W. T.** Sphaerotheca phytoptophila Kell. & Sw. Journal of Mycology. 4:93–94. 1888.
13. ——— Hackberry Witches Broom. Kan. State Agri. Ex. Stat. Rept. p. 302–315. 1888.
14. **Küstenmacher, M.** Beiträge zur Kenntnis der Gallenbildungen mit Berücksichtigung des Gerbstoffes. Jahr. f. wiss. Bot. 26:82. 1894.
15. **Kuster, E.** Pathologische Pflanzenanatomie. Jena. 1903.
16. ——— English Translation of No. 15 by Frances Dorrance, Univ. of Wisconsin, 1913. (mimeograph).
17. ——— Die Gallen der Pflanzen. S. Hirzel, Leipzig. 1911.
18. **Lacaze-Duthiers.** Recherches pour servir a l'Histoire des Galles. Ann. Soc. Nat. Bot. Ser. III Tome 19:273–354, 4 pls. 1853.
19. **Low, Fr.** Beiträge zur Kenntnis der Milbengallen (Phytoptocecidien). Verh. Zool.-bot. Ges. Wien. 28:127–150, 1 pl. 1878.
20. **Magnus, W.** Die Entstehung der Pflanzengallen verursacht durch Hymenopteren. (160 pp. 32 text figures, 4 double plates) G. Fischer, Jena. 1914.
21. **Mally, C. W.** Psyllidae found at Ames, Iowa. Proc. Iowa Acad. Sci. 1:131–138. 1893.
22. ——— Psyllidae found at Ames, Iowa. Proc. Iowa Acad. Sci. 2:152–171. 1894.
23. **Molliard, M.** Hypertrophy pathologique des Cellules vegetales. Rev. Gen. bot. 9:33–34, pls. 5–6. Paris. 1897.
24. ——— Sur les Modifications histologiques produites dans les Tiges par l'action des Phytoptus (Eriophyes). C. R. Acad. Sc. Paris. 129:841–844. 1899.
25. ——— Caractères anatomiques de deux Phytoptocécidies caulinaires internes. Marcellia, 1:21–29, 1 Pl. 1902.
26. **Patton, W. H.** A Principle to observe in naming Galls. Can. Ent. 29:247–248. 1897.

27. **Prillieux, E.** Etude sur la Formation et le Développement de quelques Galles. Ann. Sc. Nat. Bot. 3:113. 1876.
28. **Riley, C. V.** Insects injurious to the Hackberry. Part of 5th Rept. U. S. Ent. Comm. 601–622. 2 galls figured. 1890.
29. **Ross, H.** Beiträge zur Kenntnis der Anatomie und Biologie deutscher Gallbildungen, I. Ber. d. D. Bot. Ges. 28:228. 1910.
30. **Rubsaamen, Ew. H.** Die Zoocecidien, durch Tiere erzeugte Pflanzengallen, Deutschlands und ihre Bewohner. Lief. I. Stuttgart. 1911.
31. **Stewart, A.** The Anatomy of the (Andricus) Punctatus Gall. Am. Jour. Bot. 1:531–546. Pl. 2. 1914.
32. **Thomas, Fr.** Zur Kenntnis der Milbengallen und Gallmilben usw. Zeitsch. f. d. ges. Naturwissensch. 42:513. 1873.
33. **Wells, B. W.** A Survey of the Zoocecidia on Species of Hicoria caused by Parasites belonging to the Eriophyidae and the Itonididae (Cecidomyiidae) Ohio Jour. Sci. 16:37–57. 2 pls. 1915.

EXPLANATION OF PLATES.

(See also table of abbreviations following.)

PLATE XII.

Fig. A. Cross section of normal one year old stem of Celtis occidentalis in winter condition. × 170.
Fig. B. Longitudinal section of one year old stem. × 170.
Fig. C. Section of normal leaf blade. × 180.
Fig. Ca. Study of leaf vein. × 190.

PLATE XIII.

Fig. 1. Simple gall of Eriophyes sp. causing witches-broom, showing a common mode of early development at one of the nodes. 1 yr. old. × 1.
Fig. 1a. Longitudinal section through base of gall branch. × 1½.
Fig. 1b. Sketch of 2 yr. old "broom" showing relation of secondary gall branches to the primary ones. The bark has been removed. × 1½.
Fig. 1c. Detail study of part indicated at c, Fig. 1a. × 120.
Fig. 1d. Study of trachea and adjoining cells indicated in Fig. 1c. × 400.
Fig. 2. Sketch of smooth specimen of lepidopterous twig gall. × 1½.
Fig. 2a. Longitudinal section of gall shown in Fig. 2. × 1½.
Fig. 2b. Diagram of normal stem section (transverse). × 18.
Fig. 2c. Diagram of gall section (transverse). × 18.
Fig. 2d. Detail study part d, Fig. 2c. × 150.
Fig. 3. Median section through gall of Pachypsylla vesiculum. (diagrammatic). × 20.
Fig. 3a. Detailed study of part indicated at a, Fig. 3. × 100.

PLATE XIV.

Fig. 4. Gall of Pachypsylla sp. on side of stem. See also Pl. XIX, Fig. 10. × 5.
Fig. 4a. Diagram of cross section of gall and stem. × 22.
Fig. 4b. Detail of part b, Fig. 4a. × 100.
Fig. 4c. Detail of part c, Fig. 4a. × 100.
Fig. 4d. Detail of part d, Fig. 4a. × 380.
Fig. 5. Gall of Pachypsylla gemma. × 5.
Fig. 5a. Diagram of transverse section of P. gemma. × 22.
Fig. 5b. Detail of part b, Fig. 5a. × 150.
Fig. 5c. Normal bud. × 5.

PLATE XV.

Fig. 6. Gall of Pachypsylla mamma (mature). × 4.
Fig. 6a. Vertical median section through mature gall. × 4.
Fig. 6b. Diagram of a slightly immature specimen. Median, vertical section. × 36.
Fig. 6c. Detail of part c, Fig. 6b. × 85.
Fig. 6d. Detail of part d, Fig. 6b. × 85.
Fig. 6e. Detail of part near e, Fig. 6b. × 85.
Fig. 6f. Normal leaf cystolith at f, Fig. 6b. × 340.
Fig. 6g. Aborted cystolith at g, Fig. 6b. × 340.
Fig. 6h. Detail study of nutritive tissue close to blind end of apical canal, showing criss-cross thickening of cell walls. × 125.
Fig. 6i. Parenchyma and scleride cells from mature gall. × 85.
Fig. 6k. Parenchyma from leaf mesophyll. × 85.
Fig. 6m. Parenchyma from petiole cortex before thickening. × 85.
Fig. 6n. Parenchyma from twig pith. × 85.

PLATE XVI.

Fig. 7. Gall of Pachypsylla venusta. × 1½.
Fig. 7a. Longitudinal median section of P. venusta. × 1½.
Fig. 7b. Tangential section of gall, showing flocculent waxy material developed by the nymphs of P. venusta. × 1½.
Fig. 7c. Transverse section of gall. × 1½.
Fig. 7d. Detail of outer part of wall indicated at d, in enlargement near 7c. × 100.
Fig. 7e. Detail of inner part of wall indicated at e near Fig. 7c. × 100.
Fig. 7f. Lignified cell with simple pits illustrating the type of cell comprising the core of the gall. × 400.
Fig. 7g. Multicellular trichomes lining the canals leading into the chambers. See g, Fig. 7a. × 100.
Fig. D. Cross section of normal petiole. × 170.

PLATE XVII.

Fig. 8. Gall of Cecidomyia unguicola. × 6.25.
Fig. 8a. Detail study of longitudinal, median section of gall. × 36.
Fig. 8b. Detail study of a transverse section of gall taken distal from the gall base, about one-third the length of the gall. × 36.
Fig. 8c. Trichomes found in the apical canal. × 170.
Fig. 8d. Sclerenchyma and crystal-bearing cells found at proximal end of protective layer. × 340.
Fig. 8e. Sclerides of one year old stem adjoining bast fibres. × 340.
Fig. 8f. Sclerides of three year stem with associated crystal-bearing cells. × 340.
Fig. 9c. Sclerenchyma cells and crystal-bearing cells from proximal side protective layer of Phytophaga celtiphyllia (9a). × 340.
Figs. 10–10a. Phytophaga wellsi. Gall and vertical median section of gall. × 4.1.
Figs. 11–11a. Cecidomyia sp. Gall and median section of gall. × 6.25.
Figs. 12–12a. Cecidomyia sp. Gall and median section of gall. × 4.1.
Figs. 13–13a. Cecidomyia sp. Gall and median section of gall. × 6.25.
Fig. 13b. Details of distal end of median section of gall 13. × 85.
Figs. 15–15a. Cecidomyia sp. Gall and median longitudinal section of gall. × 4.1.
Fig. 15b. Transverse section of gall 15. × 6.25.

PLATE XVIII.

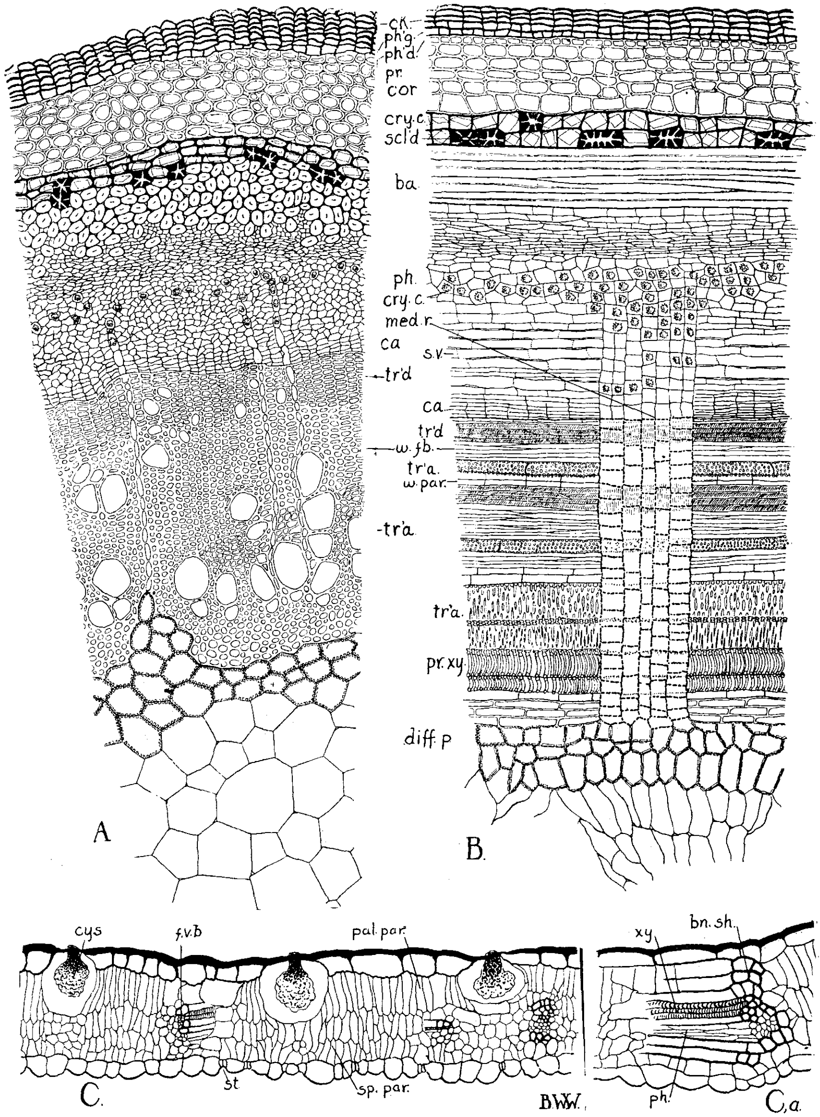
Fig. 9. Gall of Phytophaga celtiphyllia. × 6.25.
Fig. 9a. Vertical median section of gall of Phytophaga celtiphyllia shown in detail. × 36.
Fig. 9b. Details of cells found in region near b in Fig. 9a. × 140.
Figs. 14–14a. Cecidomyia sp. Gall and median section of gall. × 4.1.
Figs. 16–16a. Cecidomyia sp. Gall and median section of gall. × 6.25.

Plate XIX.

Fig. 1. Witches-broom. Gall technically confined to proximal ends of branches, inconspicuous in the photograph. × 1/4.
Fig. 2. Lepidopterous gall of lateral branch. × 1.
Fig. 3. Pachypsylla sp. Gall on side of twig. Gall broken open to show the nymph. × 4.
Fig. 4. Cecidomyia sp. Gall No. 16. An old gall whose chamber was not dropped. × 3½.
Fig. 5. Cecidomyia sp. Immature galls of No. 16 on fruit. The side of the berry has been removed to show the galls projecting into the ovulary cavity, the ovule in which remains aborted. × 2.
Fig. 6. Cecidomyia sp. Mature galls (No. 16) on twigs. Upper galls at stage in which the larval chambers are dropped; lower gall older, the tissue dying and turning black. × 1/3.
Fig. 7. Galls of Pachypsylla venusta. (gall of petiole). × 1/4.
Fig. 8. Cecidomyia sp. Immature galls (No. 16) on fruit. Normal fruit shown near it. × 1¾.
Fig. 9. Galls of Pachypsylla mamma. × 1/4.
Fig. 10. Galls of Pachypsylla gemma (bud galls) and those of Pachypsylla sp. forming ovoid lateral stem swellings. × 1/4.

TABLE OF ABBREVIATIONS.

abc. l.—abscission layer.
ab. xy.—abnormal xylem.
ab't. cys.—aborted cystolith.
ap. c. tr'm.—apical canal trichomes.
ba.—bast.
bn. sh.—bundle sheath.
ca.—cambium.
ck.—cork.
cor.—cortex.
cor. par.—cortical parenchyma.
cys.—cystolith.
cry. s.—crystal "sac."
cu.—cutin.
deh. l.—dehiscence layer.
diff. p.—differentiated pith.
epi.—epidermis.
g. cor.—gall cortex.
hyp'l. mes.—hyperplasied mesophyll.
hyp'l. ph'g.—hyperplasied phellogen.
hyp't. pal.—hypertrophied palisade tissue.
la.—larva.
l. c.—larval chamber.
l. v.—leaf vein.
lig. scl.—lignified sclerenchyma.
med. r.—medullary ray.
m. la.—middle lamella.
nut. l.—nutritive layer.
nym.—nymph.
p.—pith.
pal. par.—palisade parenchyma.
ph.—phloem.
ph'd.—phelloderm.
ph'g.—phellogen.
pr. xy.—primary xylem.
pro. l.—protective layer.
scl'd—scleride.
scl'd. l.—scleride layer.
sim. p.—simple pit.
sp. par.—spongy parenchyma.
s. v.—sieve vessel.
tr'a.—trachea.
tr'd.—tracheid.
w. par.—wood parenchyma.
xy.—xylem.



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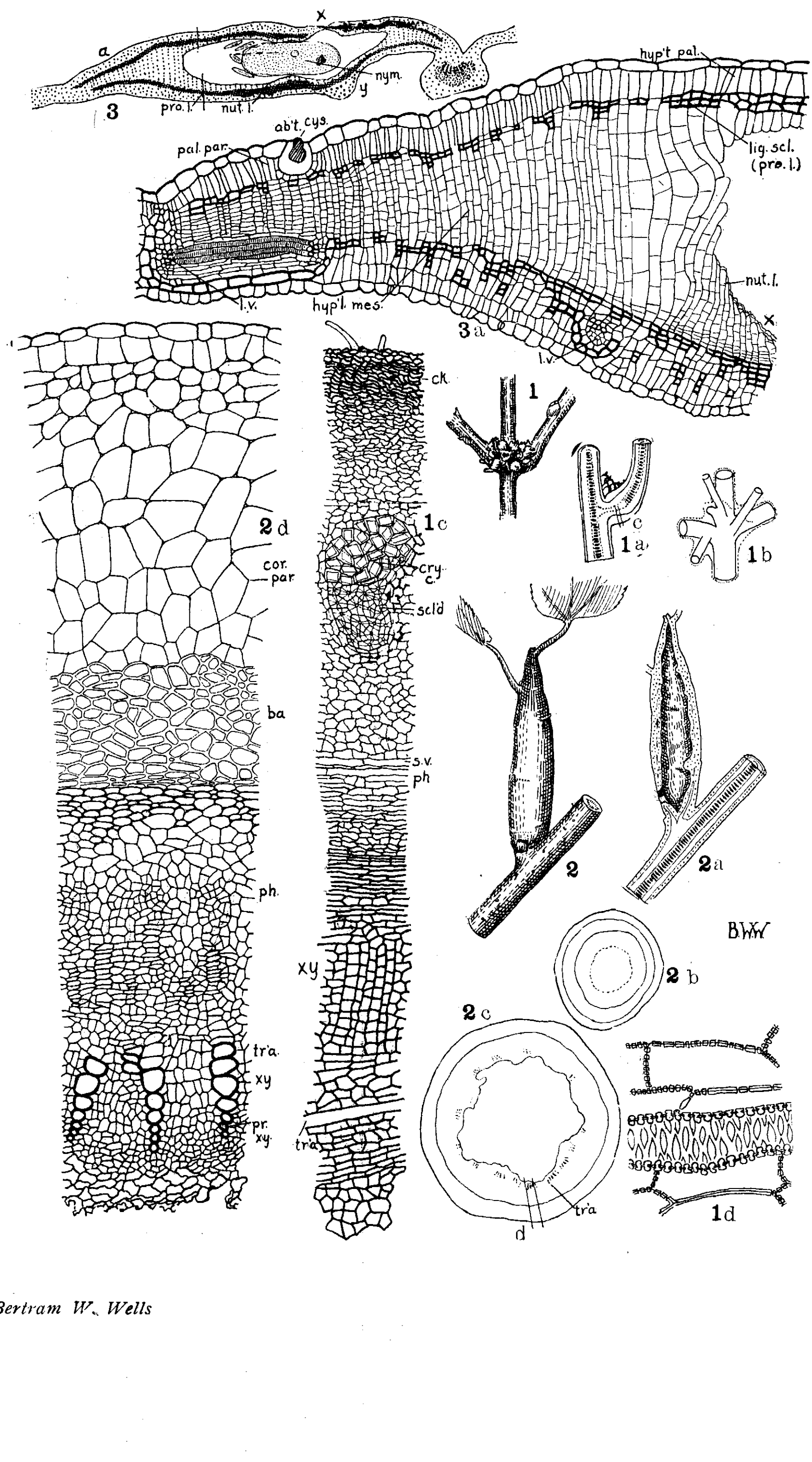

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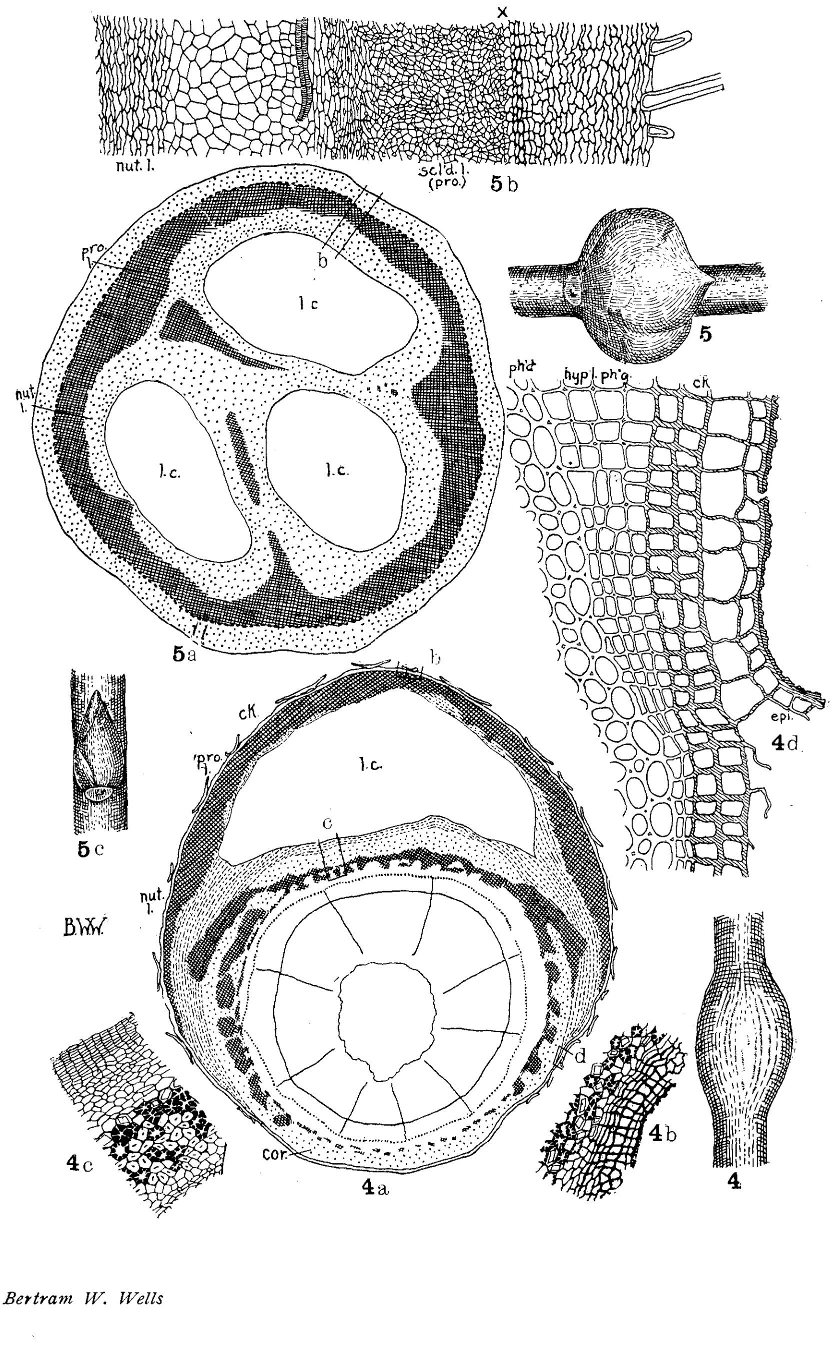

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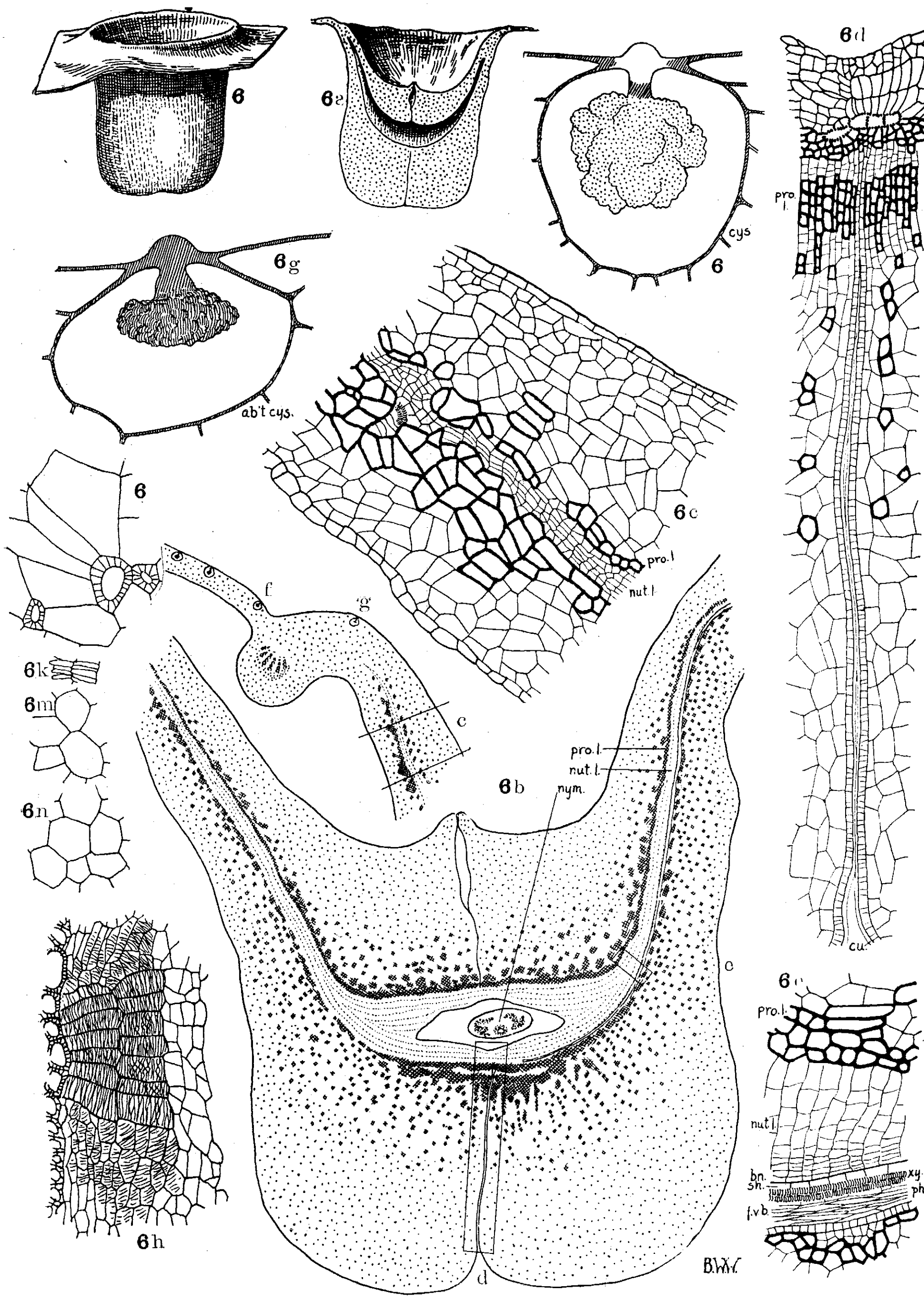

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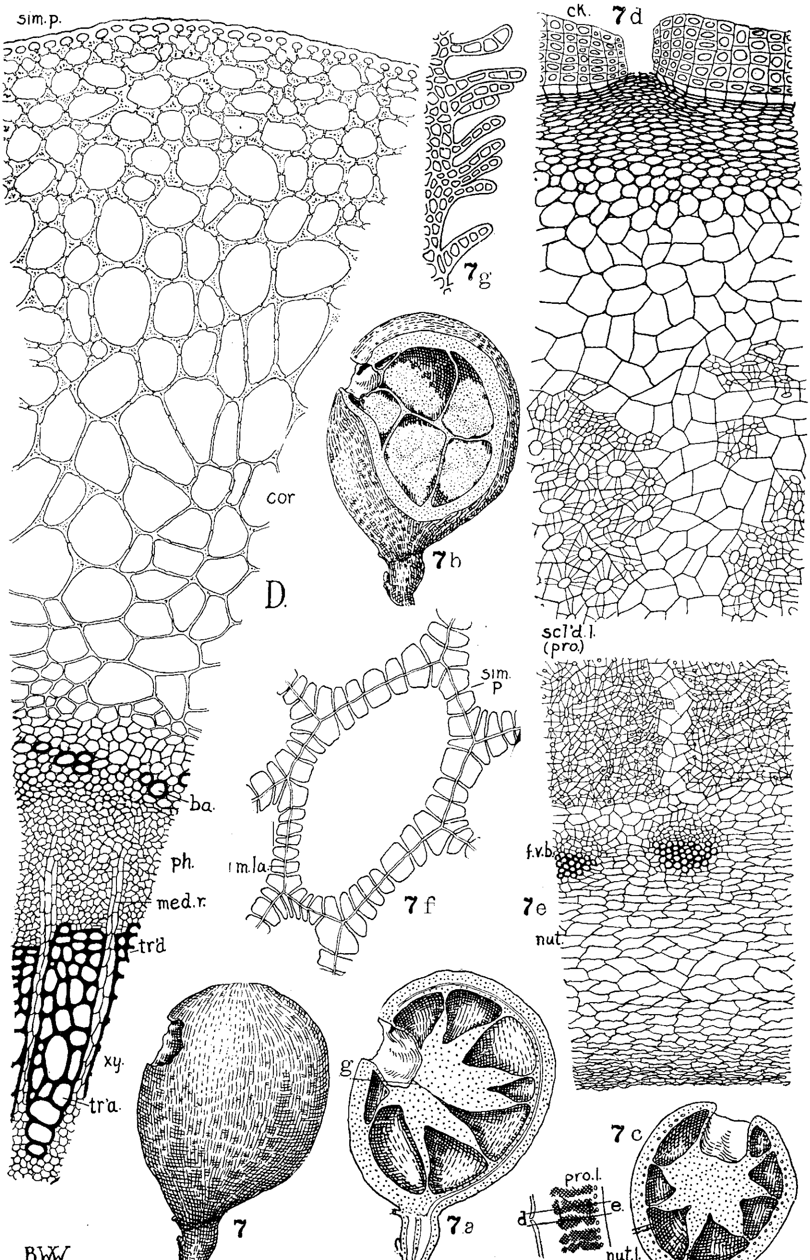

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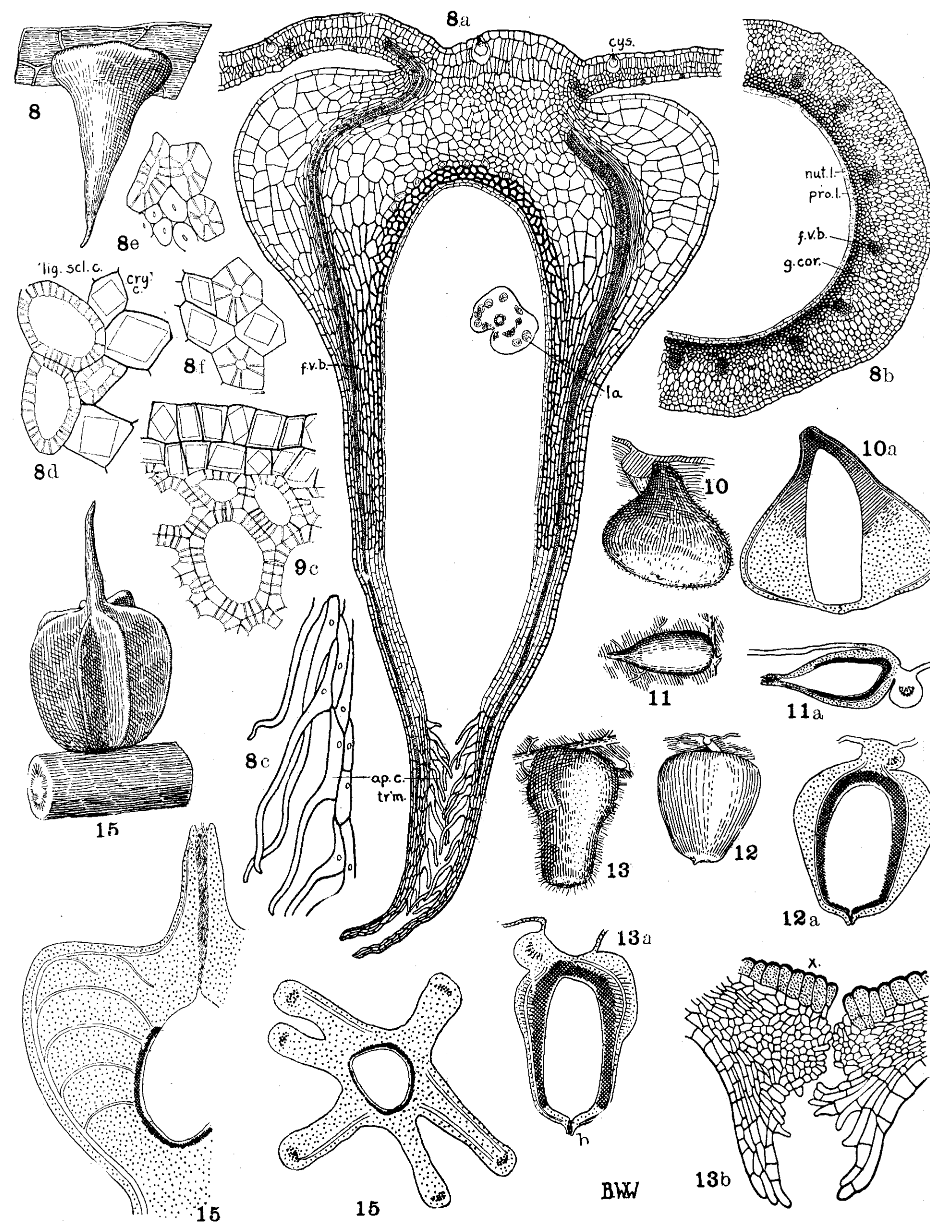

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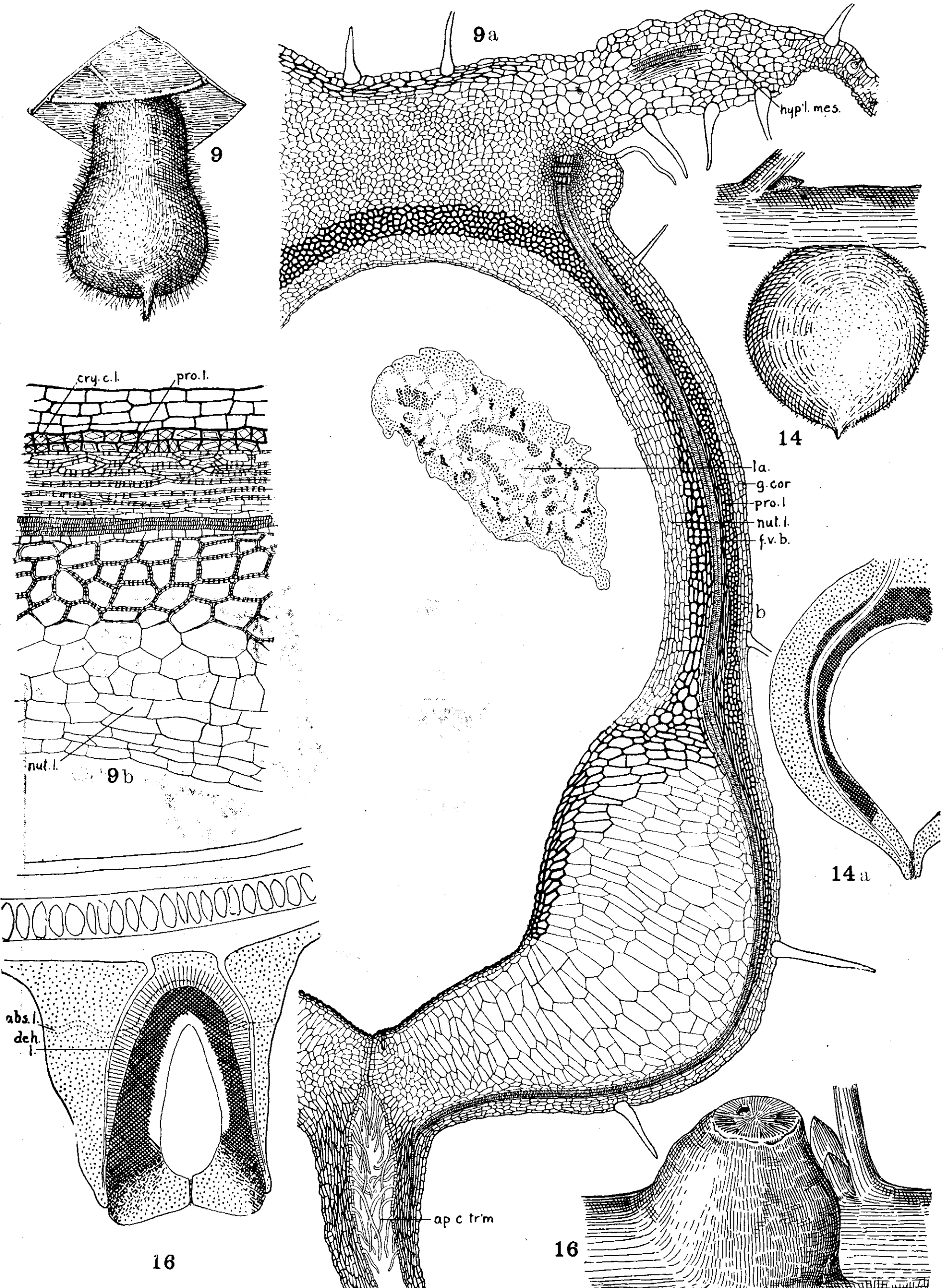

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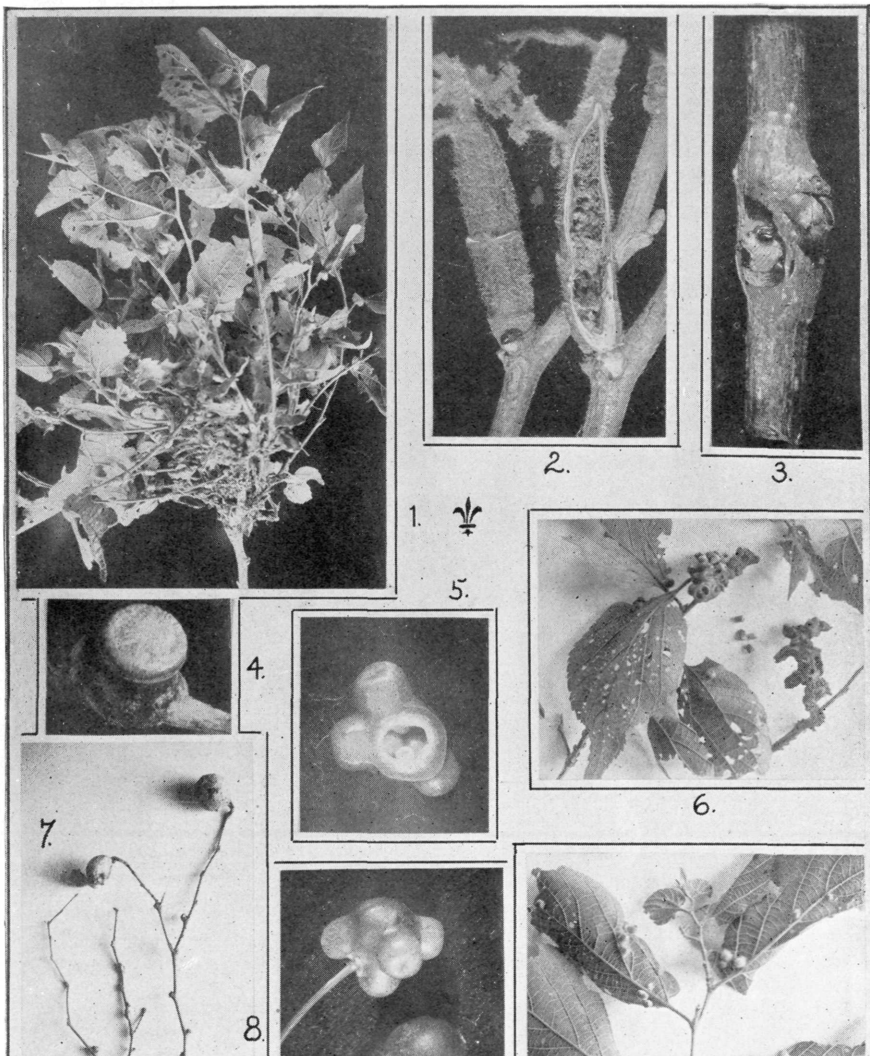

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